

THE LONGEVITY OF PLANTS

(Die Lebensdauer der Pflanze)

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Authorized English Edition

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TRANSLATOR'S PREFACE

Acknowledgements, to the reader, may appear as useless addenda, but to the writer they are the humble expression of an inescapable conviction that without the assistance of his colleagues this translation would not have borne fruition, or at least, would have entailed greater difficulties. It is in this spirit that I gratefully recognize the assistance of Dr. A. B. Stout who directed the attention of the writer to this work of Dr. Molisch, and who read the entire translation; to Dr. J. H. Barnhart for his ever-willing council in bibliographical matters; and to Mrs. A. S. Linton for her checking of the entire translation and for other details in completing the volume.

Thanks are due particularly to Dr. Barnhart who painstakingly verified or corrected every citation in the bibliography of the German edition, so far as was at all possible, and in most cases augmented the original and usually incomplete forms in which they were presented.

EDMUND H. FELLING

FOREWORD

Reports of observations concerning longevity, senescence and death among plants are so scattered in the literature, frequently in such inaccessible places, that it is difficult to orient oneself properly in the various aspects of the important problems of natural science which are involved. Because of this situation I undertook, ten years ago, to study the longevity of plants from various viewpoints and to gather the known facts, with necessary revisions, into a monograph of the problem as it concerns the entire plant kingdom.

In 1921 the foundation for this proposed book had already been completed in outline but my appointment at the Imperial University of Sendai in Japan interrupted its completion. Other duties during my almost three year visit in the Land of the Rising Sun so occupied my attention that the manuscript had to be laid aside and could not be completed until my return to available sources of the latest literature and research upon the subject. I now hope I have produced a small contribution that will be a welcome supplement to E. Korschelt's excellent book, "Lebensdauer, Altern und Tod." While Korschelt's work is concerned with the longevity primarily of animals and only secondarily with that of plants, my work is devoted especially to an account of longevity among plants without, however, entirely neglecting the general aspects of the problem as they apply to animals.

Before concluding this foreword, I wish to thank my assistant, Dr. J. Kisser, for his preparation of certain illustrations and for correcting proof which I was unable to do myself because of my call to India. My thanks are extended to Dr. W. Frenzel who, too, carefully examined the proof.

My esteemed publisher, G. Fischer of Jena, willingly cooperated as always and made great efforts toward a satisfactory completion of this little work. To him also I extend my sincere thanks.

HANS MOLISCH

VIENNA, OCTOBER, 1928

INTRODUCTION

The subject of longevity of living organisms presents an exceedingly important biological problem. In a variety of ways it touches upon so many phenomena of plant life and of biology in general that it provokes common scientific interest even beyond the realm of physiology itself.

Strange to say, no comprehensive study upon the subject has heretofore been made. Jessen's worthy contribution,¹ "Über die Lebensdauer der Gewächse," which appeared 65 years ago, did not consider the subject in its entirety but dealt with only one though very significant aspect. It was concerned primarily with the question as to whether asexually propagated seed-plants possess an unlimited tenure of life, terminated only by accident or other unfavorable circumstances, or whether their longevity is inherently limited. Other problems associated with longevity were disregarded. A careful study of the subject among both lower and higher plants was neglected and no consideration was accorded such matters, among others, as senescence, developmental changes, the death of cells and tissues in the tree, nor the possibility of curtailing or prolonging life.

Only recently has interest been focussed upon the problem, particularly by Weismann's ideas with respect to perpetual life among unicellular organisms. Many zoologists have worked upon this problem and in 1924 Korschelt² gave us an excellent summary of the understanding which prevailed at that time of longevity, senescence and death among animals. In this work longevity among plants is only incidentally considered. For the most part, Korschelt's meritorious work is concerned almost exclusively with animals and in view of this there is need of a detailed and comprehensive consideration of the subject from the botanical standpoint.

CHAPTER I

THE LONGEVITY OF UNICELLULAR ORGANISMS

PERPETUAL LIFE OF UNICELLULAR ORGANISMS

The need for an intensive study of longevity has been partially fulfilled already in zoological and botanical writings, especially by those of Doflein³ and Küster.⁴ Doflein was concerned, however, not so much with longevity itself, but rather, as the title of his book indicates, with the problem of death and perpetual life among both plants and animals. Küster presented a short survey of senescence and death, almost entirely as it concerns plants, in a contribution which evolved from a preliminary report upon the subject. And Weber's⁵ concise but very desirable physiological review of the phenomena accompanying senescence has also furnished a welcome contribution.

In spite of these valuable works, however, there is lacking a monographic study of longevity among plants and of the associated many-sided questions concerning senescence and death. In the following discussion, therefore, an attempt will be made to meet this need and to gather together in a critical fashion the pertinent and widely scattered contributions upon each phase of the subject.

It was generally believed, not so long ago, that every organism must perish at some time. For most multicellular organisms this conception still holds true, but not in the case of most unicellular forms.

Weismann⁶ performed the great service of calling attention to the fact that while we customarily associate a residual dead body with our conception of death, in the case of asexual propagation of infusorial organisms by mere cell division the entire mother-cell is transformed, without residue, into two daughter-cells. The mother-cell divides into two almost identical parts, equivalent in appearance and constitution. Each of these halves continues to live in the same manner as did the mother-cell and eventually divides in its turn. This led Weismann⁷ to conclude "that the limitations imposed upon an individual cell by death are not, as previously assumed, unavoidable and inherent attributes of its nature, but rather perform a definite function and are called forth only when

certain complications in the development of the organism would tend to interfere with its natural tendency to live forever."

As with so many other great truths, this one, too, has not entirely escaped refutation. The zoologist Wedekind¹ has been most pronounced in opposing this teaching of Weismann, though with inadequate foundation for his contentions. In his opinion, there is no basis for Weismann's premise that unicellular organisms divide into two identical parts. They only appear to do so, he contends, and, consequently, among single cells as well as elsewhere, we can speak in every case of mother- and daughter-cells. The mother-cell is capable, he admits, of dividing again, indeed repeatedly, but eventually it must perish. Were I also to concede that in many cases the resulting halves of multiplying cells are not equivalent, as I shall show is true of certain unicellular plants, it still remains for Wedekind to prove that the two halves are not equivalent in every case and that the mother-cell is not capable of dividing *ad infinitum*. No one has yet shown that the halves of dividing bacteria are not alike and the same holds true for many other unicellular organisms. The facts in every case, therefore, do not support Wedekind's refutation of Weismann's conception.

Other objections, based upon experimental grounds, are better founded. The question has been asked, Can protozoa really undergo an unlimited number of successive divisions or do they finally perish, perhaps after a certain number of generations? Maupas² was able to show by his cultures of various species of ciliated infusoria that these organisms suffered marked changes in appearance and behavior as the result of long-continued breeding. After undergoing 100 to 300 divisions, the cells began to absorb less nutriment, became smaller, lost a portion of their cilia and finally succumbed. On the basis of these observations, Maupas opposed the ideas of Weismann and defended the view that the unicellular organism is not endowed with unlimited tenure of life but finally becomes exhausted and perishes.

For further investigations along this line we are indebted to Calkins³ and to Hertwig. During the course of 15 months Calkins secured more than 500 generations of the infusorian, *Paramecium caudatum*, and, after 90 to 170 divisions, found changes in the progeny similar to those observed by Maupas. These changes, constituting what Calkins called the "depression condition," finally

led to death. The "depression" can be alleviated, however, in a variety of ways, as by conjugation, agitation, and changes in the temperature or composition of the nutrient solution. According to Calkins, the "depression condition" constitutes a part of the developmental cycle and represents a phase in the life of infusoria controlled by internal factors.

Hertwig^{11a-c} has professed a similar idea. He studied principally the changes in protista cells resulting from continued asexual propagation and regarded the concomitant alterations between protoplasmic and nuclear masses, *i.e.*, the nucleo-plasma ratio, as the controlling factor. If the normal relation between nucleus and cytoplasm is disturbed, there results, he says, hypertrophy of the nucleus and development of all those phenomena which constitute Calkins' "depression condition." Conjugation re-establishes the normal relation and without it death would ensue. Hertwig also believes that single cells do not possess perpetual life but that death is an inevitable result of life processes.

It appears, then, as if Weismann's views had been invalidated. The subsequent breeding results of the American investigator Woodruff,^{12a-d} however, placed the works of Maupas, Calkins, and Hertwig in an entirely different light and upheld to a great degree the teaching of Weismann concerning perpetual life of unicellular organisms. Woodruff began with a single *Paramaccium caudatum*, secured from an aquarium, and in the course of seven years bred therefrom 4500 generations in concave slides. Altogether, since 1907, he has secured 8000 generations without conjugation playing any part, for newly formed cells were always transferred to a fresh nutrient solution. Under these conditions there appeared no degeneration or depression and the daily number of divisions, except for certain rhythmic fluctuations¹³ which need not be discussed here in detail, remained, after thousands of generations, the same as in the beginning.

It is particularly important in such investigations that the progeny always be transferred to a fresh nutrient solution. Otherwise, the accumulation of secreted assimilation products causes those disturbances which constituted the degeneration observed by Maupas, Calkins, and Hertwig. If the accumulation of such products be avoided by constant change of solution, then, as Woodruff

has shown, thousands of generations can be secured by division alone without recourse to conjugation. And in this way the justification of Weismann's belief in the perpetual life of unicellular forms is established.

The mutual influence exerted among organisms by their secretion products is of considerable significance.¹⁴ I refer to the relation between host and parasite, and to the influence of bacteria, yeasts and molds upon the substratum. The production of either growth-inhibiting or growth-promoting substances may be involved and the former may accumulate to such an extent that further development is inhibited, a pathological condition occurs and finally the organism dies. This sequence fulfills the remark of Duclaux¹⁵ when he says "that the medium which the microbe creates for itself becomes less and less nutritive and more and more antiseptic."

Only recently have we come to realize that their own secretions are responsible for diminishing activity among infusoria. This is all the more surprising because every bacteriologist has long been familiar with the products of bacterial growth, of pigment formation and of luminescence, which accumulate in the substratum, despite a sufficient supply of nutriment. If colonies of luminous bacteria are too dense, for instance, they remain small, not only because they deprive one another of food but by virtue of the mutually inhibiting effects of their secretions. Even if we permit only a single colony to develop on a moderately nutritious substratum, it, too, finally ceases to grow and to glow because the secretions, despite abundant available food, inhibit these two functions.

Richter¹⁶ was able to make similar observations in connection with his pure cultures of diatoms. Upon his own as well as Beijerinck's findings, he concluded "that all algae, cultivated in great quantities within limited confines, show effects attributable only to secretion substances which are poisonous to the cells and which hinder their increase and growth. The need for frequent transference of the material being studied is thus self-apparent." Paramoecia are in no wise different but act in accordance with this general behavior.

To return now to the question of perpetual life among infusoria, it is apparent that conjugation is not necessary in an uninterrupted succession of even several thousand generations but that it does

serve to prevent degeneration which would ensue under unfavorable culture conditions.

There are also certain unicellular organisms which are not at all capable of conjugating but which reproduce exclusively by cell division, *i.e.*, wholly asexually. Among them are bacteria and the blue-green algae or Cyanophyceae. Without question, these may be regarded as being endowed with everlasting life in the sense of Weismann. In addition, a great many unicellular algae and fungi are known which, like the infusoria, perpetuate themselves by conjugation as well as by cell division. That they are capable of maintaining their kind by asexual means alone is indeed very likely but as yet unproven. It would be very desirable, therefore, if propagating experiments with these organisms were pursued similar to those which already have been carried out with *Paramecium*. Such experiments might easily be conducted upon desmids and in all probability they would show the same results as have those with infusoria.

As Woodruff did with infusoria, so has Hartmann¹⁷ performed propagating experiments with a green colony-forming flagellate, *Eudorina elegans*, which reproduces only asexually. Hartmann was able to pursue these experiments for ten years and claims to have secured more than 3000 generations by purely asexual reproduction at a constant rate of division and without evidence of any ill effects upon either the nuclei or the cells themselves. In view of this, we may attribute perpetual life in Weismann's sense to these green flagellates also.

Bölär obtained identical results with a zooprotistan, *Actinophrys sol*, during five years' work.

Considerable interest attaches to the fact that similar results can be secured with certain lower multicellular animals which are capable of asexual multiplication by division and by budding. Goetsch and Gross were able to propagate our common freshwater polyp in a purely asexual manner for years at a time and at a constant rate when kept under uniform conditions. Hartmann secured similar results with a certain planarian, *Stenostomum*, as did Hämmerling with the oligochaete, *Aelosoma*, without evidence of physiological decadence if only the same favorable conditions were uniformly provided.

ARE ALL UNICELLULAR ORGANISMS ENDOWED WITH PERPETUAL LIFE?

Zooprotistans—Weismann's conception of perpetual life among unicellular organisms is frequently represented as to imply that all single-celled forms are so endowed. Such generalization is, of course, unjustified. Hertwig and Korschelt¹⁸ have already noted this in the case of animals and I shall show that it pertains also to plants. Hertwig called attention to the decline of the larger part of the nucleus during cyst formation among the heliozoa and refers to such processes as "partial death" among unicellular organisms. Among other protozoa, as in the case of *Noctiluca*, a part of the cell body remains as a lifeless residuum after formation of a great number of swarm spores. In the case of certain protozoa which are provided with a shell, various portions of the cell degenerate. Korschelt brought this out and remarks "that these parts may no longer be of service in cell division and though employed for whatsoever purpose during normal vegetative life, they have served their function and are discarded by the animal, as is true also of the eyelash and other parts of the body."

The newer investigations with protista have shown that lifeless bodies may actually appear, even resembling the cells in form. This is particularly true during reproduction of larger multinucleate forms when they break up into a number of uninucleate reproductive bodies corresponding to the original number of nuclei. That death ensues upon such continual vegetative propagation is especially well shown by the multinucleate radiolarians whose form and structure are so remarkable. Their marvelous organization is destroyed and certain nuclei and portions of the individuals become lifeless. This is true of all protista with multiple reproduction. All transitions among these lifeless units may be recognized, from those closely resembling a cell to enucleated structures. As Hartmann correctly noted, we observe here the termination of one individual development as the result of propagation and the initiation of a new development, so that we may in truth speak of the death of an individual.¹⁹

The question has also been raised as to whether the cell, endowed with perpetual life, does not change in some way during its life and then become rejuvenated by propagation. In attempting to

suppress reproduction, Rubner²⁰ investigated this question so far as it concerned yeast cells and Hartmann²¹ studied it in *Gonium pectorale*. Rubner attempted to hinder reproductive growth of the yeast by controlling nutritional conditions without, however, interrupting other life processes. Under these conditions the fermenting power remained unchanged the first four days and then fell off, growth ceased and finally the yeasts died. Without growth and budding, the life of the yeast is then of limited and relatively short duration. Hartmann experimented with *Gonium*. In the case of this alga, individuals of four times normal size could be cultivated in concentrated solutions of nutritive salts. They lived for several weeks in contrast with normal ones which reproduced within one or two days. This experiment finally resulted in the death of those cultures in which propagation was prevented. All this indicates strongly that unicellular organisms undergo alterations during their lives as individuals and that by vegetative reproduction there ensues a rejuvenation of the cell plasma.

Hartmann has succeeded in showing by an interesting and very significant experiment that the rejuvenating influence of propagation can be secured also by periodically repeated amputation with resulting regeneration. When the forward end of the multicellular planarian, *Stenostomum leucops*, was amputated 52 consecutive times, it could be kept alive for 13 months, a period during which 41 divisions occurred among sister animals. Similar results have been secured with the infusorian, *Stentor coeruleus*, and with two species of amoeba, *A. Proteus* and *A. polyzona*. Hartmann²² was able to bring one individual of *A. polyzona* through 32 amputations and subsequent regenerations during a period of 42 days in which time another individual of the same lineage divided 15 times. Under certain culture conditions, *Amoeba proteus* divides every second day and in the case of this species the afore-mentioned author succeeded in prolonging the life of one individual as long as 50 days by means of 52 amputations. Hartmann is of the opinion that by continuing such procedure the life of these organisms can be prolonged indefinitely. The rejuvenation which accompanies normal reproduction can thus be brought about by reduction of the body through amputation.

Hartmann believes that such amputation prolongs life by the facilitated exit it provides for secretion of materials from the ampu-

tated body. Whether this is actually the case is still a question because, in my opinion, wound hormones formed at the wounded surface might have a rejuvenating influence just as they do among higher plants.

Hartmann's amputation experiments have demonstrated the potential perpetual life of protozoan cells and have shown at the same time that the cell itself changes and that the symptoms of senescence are alleviated by vegetative reproduction. Vegetative reproduction, then, really brings along with it a rejuvenation and in these investigations amputation replaced it and produced the same effect.*

Diatoms—So far as I know, botanists have not been concerned hitherto with Weismann's idea of perpetual life as it concerns diatoms and certain other unicellular plants. In their case the entire subject needs further elucidation and the following discussion will be devoted, therefore, to these forms. On the basis of intensive studies by Pfitzer²⁶ and others, we know that the special cell wall of the diatomaceous cell consists of two halves which fit one within the other as do the two halves of a pill-box. Both halves are silicified to such a high degree that when once fully formed they are incapable of further growth and preserve all their structural features even after being heated.

When a diatom divides, the two shells or valves are pushed apart by the increasing mass of protoplasm and each daughter-cell receives from the mother-cell one old half-shell and the other half-shell must be formed by the daughter-cell.

As a little reflection will reveal, the newly formed daughter-cells must accommodate themselves to the fact that the old fully developed halves are incapable of further growth because of their great silicification. One of the daughter-cells, accordingly, is as large as the mother-cell, the other smaller. Since the newly formed shell of the latter fits within the older shell, the cell itself is shorter than the mother-cell around the double thickness of the membrane and, according to the binomial theorem and on the presumption that all

* Bacteria, too, can alter their characteristics during the course of their individual lives. As an example, young cells are often more sensitive to high temperatures than old ones. It has been shown in investigations upon the heat resistance of high temperature-preferring and high temperature-resistant bacteria, isolated from milk, that young bacteria die at relatively lower temperatures than do the old ones. This was demonstrated for *Microbacterium lacticum*, *Sarcina lutea* and *Streptococcus thermophilus*.^{22a}

cells divide equally, it can be expected that within a relatively brief period there will arise very short cells.

This continuous dwarfing process naturally can not continue indefinitely. Sooner or later there must be a re-establishment of the original size and this is consummated by conjugation or by formation of auxospores. According to the species, it may be accomplished in a variety of ways but only the following cases will be cited. Two individuals lie side by side, their protoplasts fuse together after separation of the two valve-halves and eventually form the auxospore which then enlarges considerably until it acquires the original size of the diatom. This is the course of conjugation in *Surirella*. As may be noted in figure 1, two cells approach one another until their narrow ends touch. The half-valves then separate and the two protoplasts fuse into a rapidly enlarging auxospore. In *Rhopalodia* and numerous other named diatoms, copulation is accomplished in a different manner. Two cells lie together, the valves separate through a gelatinous formation, each protoplast divides into two daughter-cells, and the four cells thus formed fuse in pairs, forming two auxospores. The latter then increase in bulk up to the maximum size characteristic of their species. By these auxospores the previously described progressive reduction in size is brought to a definite though variable limit and the original size of the diatom is restored.

In addition to this sexual formation of auxospores, an asexual type is found in various diatoms. These asexual

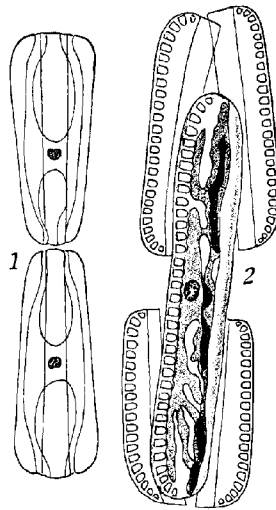


FIG. 1. *Surirella Saxonica*. Auxospore formation. 1: Two cells have approached one another with their narrower sides meeting, for the purpose of fusing; 2: the resulting auxospore. From Karsten.

auxospores are formed by division of a cell into two daughter-cells which then enlarge directly into auxospores, as in *Synedra* and *Rhabdonema*; or, as in *Melosira*, the cell may become an auxospore by merely resuming the original size after shedding its valves.

In either case, whether auxospore formation be sexual or asexual, the two silicified half-valves of the mother-cell are discarded. Can these valves then be regarded as lifeless remains and the diatom looked upon as possessing only limited tenure of life? If we regard the silicified envelope of the living diatom as actually dead matter, serving merely as a shell around the living mass, then it does not die but may be discarded during auxospore formation as an already dead structure: no part of the living protoplasm ^{as} then be said to die.

All this leads to the following conclusions: 1) Because the ^{as} cells of successive generations must become smaller and smaller, it is impossible for division of diatoms to continue indefinitely. This is in contrast with the situation among bacteria, many algae and infusoria. 2) The original size of the diatom is restored by formation of the auxospores. Whether the diatom reproduces by cell division or by auxospores, the protoplast lives on, possessing perpetual life.

Other Unicellular Algae—There are certain green unicellular forms which discard their membrane when they reproduce by conversion of their protoplasm into zoospores or aplanospores; sometimes even their flagellae and other parts are lost. If the membranes are to be regarded as structures that once were alive, we can not look upon these forms as possessing perpetual life in Weismann's sense of the term.

Botrydium granulatum is a small alga living upon damp soil and consisting of a green vesicular aerial portion and a colorless root-like subterranean part. Its mode of reproduction is asexual and consists of internal formation of a great number of zoospores which escape and develop into new plants. The old mother-cell remains, however, as a lifeless membrane with various contents.

Among the Volvocales I want to refer only to *Haematococcus pluvialis* and *Chlamydomonas nivalis*, and among the Protococcales to *Chlorococcum humicola* and to *Chlorella vulgaris*. They may well be considered here as examples of these two groups.

Haematococcus pluvialis, an alga occurring frequently in rain puddles, produces several swarm-cells just as does *Chlamydomonas nivalis* which causes 'red snow'. These swarm-cells are liberated by a bursting of the membrane and then develop into cells resembling the mother-cell. This form can reproduce also sexually by the formation of many biciliate similar gametes which fuse after being discharged. *Chlorococcum* produces a number of zoospores by internal divisions, and *Chlorella*, that widely distributed alga which is so frequently encountered in symbiotic relationship with the protoplasm of infusoria, planarians, *Hydra* and *Spongilla*, breaks up into two, four or eight aplanospores which then surround themselves with walls.

In all these cases the wall of the mother-cell remains behind with various other residua after escape of the spores. Here, then, we can not say that the entire contents of the mother-cell are transformed into daughter-cells.

Among higher plants, too, partial death is not unusual. When in autumn of every year the leaves fall from the trees and then perish; when the tree discards its bark and thereby sheds dead tissue; when tissues die in the forming heartwood of a living tree and become laden with decomposition products; when foliar pubescence is shed naturally or when the hairs become filled with air; or when floral organs are discarded; in all these cases, death of a part of the individual is involved.

Yeasts—The yeast is a unicellular fungus. Its multiplication is accomplished usually by budding which involves the formation of a bulge at any point in the wall that gradually enlarges, separates from the mother-cell and finally becomes independent by complete abstriction. The entire process is known as budding and the daughter-cells as well as the mother-cell are capable of repeating the procedure.

This process is somewhat different, however, from that which prevails in the division of bacteria or of a paramaecium. In the budding of yeast the mother-cell does not divide into two daughter-cells but abstricts a new daughter-cell so that the budding process results in the preservation of the original old cell and the formation of a new one. Since the nucleus divides in this process, the two resulting cells probably acquire equivalent nuclei and, in many cases, equal amounts of protoplasm. The walls, however, certainly

differ with respect to age, for the abstricting cell retains the old membrane and the abstricted cell acquires a new wall. In other words, in the budding method of reproduction among yeasts the mother-cell does not resolve into two equivalent daughter-cells. In this type of division we can not, however, speak of a lifeless residue, for the mother-cell can repeatedly produce more cells by abstriction. Whether the mother-cell can continue this process indefinitely—always provided, of course, with fresh nutrient solution—or can do so for only a certain length of time, has not been experimentally examined. The question as to whether yeasts possess perpetual life has not been answered, consequently.

It is well known that under special conditions involving frequent access of oxygen, favorable temperature, and deficiency of food, many yeasts form asci, similar in external appearance to the normal cells but which form a few ascospores. The latter are eventually liberated, forsaking the old cell together with its wall and other remains which then perish. It is not very likely, however, in view of the foregoing, that ascus formation is essential in the development of yeasts, for many species never form ascospores at all and those that do may lose the ability without suffering thereby. We can hardly be misled, therefore, by the postulation that ascospores are merely a type of resting spore, enabling the yeast to remain dormant as long as possible and in this condition to tide over unfavorable conditions.

Summary—Weismann's idea that unicellular organisms can continue living indefinitely holds true for most unicellular plants. It is certainly true of bacteria and blue-green algae which reproduce only asexually by division and without limit for countless generations.

Diatoms, however, can not multiply indefinitely by division because, in view of their construction, they always become smaller and smaller and must, from time to time, produce auxospores in order to restore the original size of the species. Though they discard their old siliceous armor in this process, we can not speak of death in their case because these shells in themselves are dead material; nothing is lost from the living protoplasm by either division or auxospore formation and the diatoms, therefore, may also be regarded as everlasting.

The situation is different, however, among those unicellular algae

during whose reproduction not only the wall of the mother-cell, but other cell constituents as well, die and are discarded. In these cases we already perceive a partial death and, recognizing that some portions of the organism die, we can no longer speak of an unlimited hold on life.

Our investigations also show that among plants death is not a general characteristic of living matter (bacteria, Cyanophyceae, etc.) but that it just begins to develop in certain unicellular forms in that isolated portions of the cell die during reproduction and remain as dead residue.

LENGTH OF GENERATION, DAILY PROGENY, INDIVIDUAL LONGEVITY

Whenever mention has been made in the foregoing of perpetual life among single cells it has not been implied that they are incapable of dying. Every unicellular organism can experience conditions under which it eventually dies. Many bacteria, algae, infusoria and flagellates can not endure drying out. Many succumb to cold and all succumb to heat between 100° and 150° C. and to various poisons and other unfavorable factors. In these cases the individual usually remains as a dead body; therefore, we may speak of death among unicellular forms. Only when such injuries are avoided and multiplication proceeds unabated, is the living substance of the mother-cell continually transferred by division into daughter-cells. This multiplication proceeds at different rates among different forms, exceedingly rapid as in many bacteria and yeasts, moderately rapid, or slowly as among flagellates, diatoms and infusoria.

Before discussing this further it will be well to refer to some important conceptions which occasionally are not clearly distinguished from one another. I have in mind length of generation, daily progeny, and individual longevity.

Length of generation is the time within which an individual divides, i.e., the lapse of time from the initiation to the conclusion of a division. *Daily progeny* is the number of descendants arising from any one cell during a day. *Individual longevity* of a cell is the lapse of time from one cell division to the next. In rapid cell division one division may follow directly upon the completion of

the preceding and then the individual longevity becomes reduced to nil or to a minimum.

Concerning the correlation between longevity and external injurious factors and decrease of resistance, the reader is referred to Pütter.²⁴

Bacteria—According to prevailing views, a bacillus of the common saprophytic type divides under favorable conditions more or less every 20 or 30 minutes.^{25a, b} Such a rate must be regarded as very rapid because we know of no other form of life, at least in the light of recorded observations, which multiplies so rapidly as do bacteria. Their daily progeny is extraordinarily large and their individual lives, accordingly, are very short. This is not always true, however, for many bacteria, even under favorable conditions, grow very slowly. The daily progeny of tubercle bacilli must be much less, as is indicated by the slow development of colonies. Food, temperature, light, assimilation products and other factors certainly exert great influence upon the rate of numerical increase so that the daily progeny even of the same species is not always constant but very variable.

If unfavorable conditions prevail, bacteria may experience starvation or begin to suffer from their own excretion products. In such cases they produce resting spores which, as the name indicates, can long exist as individuals until under favorable circumstances they again begin to divide. I shall refer to this in the discussion of apparent death.

Yeasts—The rate of multiplication among yeasts appears markedly lower than among most bacteria but as contrasted with other unicellular forms it is of considerable magnitude.

The duration of a generation, *i. e.*, the period of time requisite for full development of a daughter-cell which originates by budding of the mother-cell, can be determined by direct observation in a hanging drop or by calculation according to Basenau's²⁶ formula. This states that

$$x = \frac{t \log 2}{\log b - \log a}$$

where *a* represents the original number of cells, *b* the number of cells secured and *t* the duration of the investigation. The formula is valid, however, only under the assumption that the length of

generation during the entire time t is the same for every cell of the culture and that each new daughter-cell immediately begins to bud. Especially is the latter of these conditions frequently lacking, whereupon the length of generation, calculated according to the formula, is too great.²⁷

Pedersen^{28, b} determined the length of generation in the beer yeast under different temperatures and secured the following values during the first 24 hours of development:

LENGTH OF GENERATION OF BEER YEAST

| Temperature | Duration of generation |
|---------------|------------------------|
| 4° C. | 20 hours |
| 13.5° C. | 10.5 " " |
| 23° C. | 6.7 " " |
| 28° C. | 5.8 " " |
| 34° C. | 9 " " |
| 38° C. | No budding. |

By using gelatine and the same formula, Hoyer²⁹ secured the following:

LENGTH OF GENERATION OF BEER YEAST

| | Length of generation | |
|---|----------------------|---------------|
| | 13° C. | 25° C. |
| <i>Saccharomyces Pastorianus</i> I Hansen | 6 Hr. 6 Min. | |
| <i>Saccharomyces Pastorianus</i> II | 8 " 45 " | 5 Hr. 12 Min. |
| <i>Saccharomyces Pastorianus</i> III | 8 " 39 " | 6 " 8 " |
| <i>Saccharomyces ellipsoideus</i> I | 9 " 4 " | 6 " 12 " |
| <i>Saccharomyces ellipsoideus</i> II | 8 " 49 " | 6 " 9 " |
| <i>Saccharomyces anomalous</i> | 5 " 12 " | |
| <i>Saccharomyces Ludwigii</i> | 8 " 10 " | |
| <i>Saccharomyces membranaceus</i> | 7 " 1 " | 5 " 13 " |
| Yeast Saaz | 7 " 48 " | 4 " 23 " |
| Yeast Froberg | 7 " 21 " | 4 " 18 " |
| Yeast apiculatus | 4 " 45 " | |

The above data indicate that under favorable conditions the lengths of generation of different species of yeast vary from four

to nine hours and are influenced to a great extent by temperature. Further experimentation will certainly show here also three cardinal temperatures with respect to length of generation and the latter will be shortest at a particular intermediate point, the optimum temperature.

If the propagation takes place within a limited space, deficiencies of food, and poisonous secretion products will soon exert an influence to such a degree that the rate of multiplication will progressively decrease and finally become nil. It may be mentioned, incidentally, that other factors also can influence the length of generation, *e.g.*, the composition and concentration of the substratum, light and the age of the budding cell.

How long does the yeast cell remain viable and capable of further development when external conditions render budding and spore formation impossible? We must here distinguish between yeast cells under dry and those under moist conditions. Many lands are very susceptible to desiccation and the longevity of the individual is very short. Brefeld has shown that dried cultures of yeast lose their ability to multiply after 14 days. According to Hensen, yeast kept between sterile blotting paper remains viable at times for 5 to 20 months. Four years has been recorded as the longest period of viability for dried vegetative cells of a wine yeast and five years for its spores.³⁰ Yeast spores generally retain viability longer than common bud cells and in this respect resemble resting spores of bacteria.

Under moist conditions the longevity of yeast cells is considerably shorter and is dependent upon water content, the particular strain and the individual cell itself. Lafar says: "Few resistant cells long outlive the main mass. The inherent nature of the new breed likewise determines whether its longevity will be longer or shorter. The lower the temperature at which the cells are held, the longer do they remain viable. Hennenberg has shown that 12° C. is considerably more unfavorable than 7° C. At 7° C. and after 120 days a fifth of the cells still remained viable in the case of Froberg yeast. At 22° C. this strain lived about three weeks; at 30° C. it lived less than one week, and strains II and XII, as in the case of Froberg yeast, lived about three weeks at 22° C., though to a slight extent as 'reserve cells.' In cultures of dense masses the cells generally die earlier than in thinner masses, probably as the

result of an accumulation of metabolic products. For the same reason cells within the mass die earlier while those on the surface live longer. The longevity of yeast is relatively short, therefore, when the cells are saturated with water."³¹

Such observations may be of practical value because, as is well known, yeasts are grown commercially and the most suitable means of preserving them in living cultures is of importance for both the brewery and the home.

Peridiniidae—We are indebted to Hensen³² for observations concerning the rate of multiplication among the Peridiniidae. In order to determine the daily increase by division, he employed the same formula which is used in the calculation of compound interest, applying the interest rate not for the year, however, but for the day. If A represents the initial capital, r the interest rate, n the number of days during which the capital bears interest, and C the total of both capital and compound interest, the formula reads

$$C = A e^{rn}$$

or, logarithmically stated:

$$\frac{\log C - \log A}{n} = \log e^r$$

If we decrease the interest rate, or rate of increase, by one, we obtain the interest.

On the basis of numerous calculations, Hensen found the rate of increase among Peridiniidae to average 1.2. This means that each cell divides on the average after five days. If the Peridiniidae divide once within five days, the daily progeny of the mass regularly amounts to one-fifth of the entire mass.

Diatoms—Using Apstein's plankton catches, Hensen has calculated also the rate of multiplication among diatoms and has found it to be similar to that of the Peridiniidae, namely, 1.2 or 1.25, involving, therefore, a division every four days.

Benecke³³ attempted to determine the rate of multiplication among colorless diatoms in hanging drops. For this purpose, *Nitzschia putrida* is well suited. A piece of yeast scum, beset with colorless specimens of *Nitzschia* or a particle of slime, was placed upon a cover glass in a hanging drop and observed directly under the microscope. The author himself says he was not successful in securing consistent results, obviously because of other conflicting

organisms which developed at the same time in the drop. He confines himself, therefore, to the statement that "the most rapid multiplication was exhibited by two specimens of *Nitzschia putrida* in one culture which within a week's time divided twice. On April 7 two specimens were to be seen in the drop and eight on the 14 (at room temperature and in darkness)."

Also Karsten³⁴ made extensive observations on the rate of multiplication. They are all the more significant since they were conducted with various species and under a variety of culture conditions. They indicate, accordingly, how greatly the rate is influenced by the composition of the nutrient solution and by other external conditions such as light and darkness. The cultures were grown partly in glass boxes, partly upon concave slides and partly in hanging drops. For further details the original account should be consulted, but the results of Karsten's work as indicated in the table on page 27 may be emphasized.

This table indicates that the daily progeny of Peridiniidae, as determined by Hensen, is often surpassed and that in the case of the colorless and exclusively saprophytic *Nitzschia putrida* a value as high as 3.16 may be obtained which means that these diatoms may produce at their best as many as 2.16 individuals per day. Karsten remarks in this connection, however, that, since for his investigations only rapidly increasing forms were studied and all slowly growing ones were disregarded, a daily progeny of 1.2 may be regarded in general as a better average of multiplication among unicellular plants.

This conclusion appears to me too broad in its generalization, for bacteria also are unicellular organisms and many times exhibit a much greater daily progeny than 1.2. Even among diatoms this rate of increase may be too low in many and perhaps in most cases. Richter³⁵ has determined the daily progeny of *Nitzschia putrida* in carefully conducted pure cultures and found a much greater value. According to this author, it divides once every five hours during the second day. This striking difference in the findings of Benecke and Karsten on the one hand and of Richter on the other is to be accounted for, according to Richter, by the fact that Benecke and Karsten worked with ordinary cultures while he employed pure cultures. Richter ventures to say that continued increase of bacteria in ordinary cultures is hindered by their own secretions.

DAILY PROGENY OF DIATOMS

| | Daily progeny | |
|-----------------------------------|---------------|----------|
| | Light | Darkness |
| <i>Navicula perpusilla</i> | 1.26 | 1.19 |
| <i>Nitzschia Palea</i> | 1.18 | 1.09 |
| | 1.28 | 1.17 |
| | 1.16 | 1.36 |
| | | 1.17 |
| | | 1.36 |
| | | 1.21 |
| | | 1.11 |
| <i>Nitzschia Closterium</i> | 1.65 | 1.65 |
| | 1.26 | 1.60 |
| | 1.84 | 1.56 |
| | | 1.58 |
| | | 1.68 |
| | | 1.41 |
| <i>Nitzschia dubia</i> | 2.42 | 0 |
| | 2.00 | 0 |
| | 1.36 | 0 |
| | 1.47 | 0 |
| | 1.85 | 0 |
| <i>Nitzschia putrida</i> | 2.08 | |
| | 2.23 | |
| | 1.91 | |
| | 2.64 | |
| | 1.87 | |
| | 1.58 | |
| | 3.16 | |
| | 2.74 | |
| | 1.87 | |

Desmids—We are indebted to Andreesen³⁶ for information concerning the length of generation among these algae. The rapidity of cell division varies according to the nutrient solution and the individuality of the cells. When provided with leucine, albumin, dung extract or pea decoction, i.e., when under favorable nutritional conditions, the length of generation of *Closterium moniliforme* is about two days. From the initial stage of abstriction to the formation of a fully developed daughter-cell is a period of about one day.

In the case of *Cosmarium Botrytis* the length of generation varies, according to the nature of the solution, from 2 to 3.5 days.

Hyalotheca dissiliens required four to five days for a doubling of the number of cells in a filament. The length of generation of a single cell of this alga could not be determined with certainty but, according to Andreessen, it amounts to 48 hours in this genus also.

Flagellates—Certain flagellates, such as *Euglena gracilis*, likewise show a relatively high rate of multiplication,³⁷ particularly when provided with mixotrophic nutrition. This accounts for the frequent exceedingly abundant and rapid appearance of *Euglena* and other micro-organisms in manure puddles. In water barrels to which cow dung had been added to secure a good fertilizing water, I have often observed *Euglena viridis* appear in such great abundance that the upper layers were composed of a deep green creamy mass, almost exclusively of *Euglena*.

Summary—Everything taken into consideration, our knowledge of the length of generation, of the daily progeny and of the individual longevity of unicellular organisms is still exceedingly incomplete. In contrast with the great number of existing species of unicellular forms, the number of pertinent observations appears markedly insignificant. Furthermore, our information concerning length of generation or daily progeny gives nothing definite regarding individual longevity. To shed light upon this point, further extensive observations on the various groups of the simplest organisms must be made.

For convenience, our knowledge concerning length of generation and daily progeny among fungi, algae and certain other organisms may be summarized according to the table on page 29.

From this table it appears at first sight that the length of generation among unicellular organisms increases with increase in size. Bacteria, as the smallest, exhibit a very short division period and the relatively large Peridiniidae and diatoms show a much longer period. However, though the length of generation may be correlated with size, it does not appear dependent upon size alone, for the comparatively large amoebae and cells of staminal hairs in *Tradescantia* (length of generation: 80 minutes), though they are quite large, nevertheless possess a short division period. Other factors also must then control the length of generation. A satisfactory answer as to what these factors may be will be secured probably only when abundant material of the most varied unicellular forms becomes available for study.

LENGTH OF GENERATION AND DAILY PROGENY IN UNICELLULAR ORGANISMS

| Class | Species | Length of generation | Daily progeny | Time after which a division took place | Author |
|-----------------------|---|----------------------|---------------|--|---|
| Bacteria | <i>Vibrio cholerae</i> ²⁸ | 20-30 Min. | | | A. Fischer |
| | <i>Bacillus coli communis</i> ²⁸ | 20 Min. 25 Min. | | | |
| Yeasts | | | | | |
| Peridiniidae | | | | | |
| Diatoms | <i>Gyrodinium</i> ²⁹ | 4-20 Hrs. | 1.2 | 5 days | R. Petersen, <i>et al.</i> V. Hensen E. Küster V. Hensen |
| | <i>Nitzschia</i> | 24 Hrs. | 1.25 | 4 days | |
| | " <i>Palca</i> | | 1.26 | 3.8 days in light | |
| | " <i>Clusterium</i> | | 1.19 | 5.2 days in dark | |
| | " <i>dubia</i> | | 1.58 | 1.7 days | G. Karsten |
| | " <i>putrida</i> | | 2.30 | 22.8 hrs. | |
| | " <i>putrida</i> | | 2.23 | 19.4 hrs. | |
| Desmids | <i>Clusterium</i> | | | 5 hrs. | O. Richter |
| | <i>Cosmarium</i> | | | | A. Andreesen |
| Amoebae ²⁸ | | 48 Hrs. 10 Min. | | | A. Fischer |

CHAPTER II

THE LONGEVITY OF MULTICELLULAR ORGANISMS

The body of a many-celled plant is composed, as is true of similar animals, of two kinds of cells, body or somatic cells and reproductive cells. In many lower plants the difference may not always be great but with progressively increasing division of labor it becomes more apparent. The distinction may be observed clearly, however, among certain plants of relatively primitive organization, as in many of the Volvocales.

The green alga *Volvox* forms hollow globular colonies consisting of many protoplasts which are connected with one another by fine protoplasmic threads. The cells are not alike, however, but are differentiated into body and reproductive cells. The latter constitute spermatozooids and egg cells. The male sex cells arise by division of colony cells into numerous daughter-cells and appear as minute biciliate motile cells while the eggs represent enlarged green immotile colony cells surrounded by a mucilaginous substance.

Fusion of an egg cell with a spermatozoid within the globular colony gives rise to an oospore which later forms a new colony. *Volvox* can reproduce also asexually by development of daughter colonies through division of colony cells.

The reproductive cells are the evidence of continued regeneration while the residual body cells represent the transitory stage. This is true not only of the simple *Volvox* but also of the higher fungi, mosses, ferns and trees. I am in complete agreement with Weismann when he looks upon death, in the last analysis, as a means of expediency and says that he does not believe that "life has only a certain period of existence merely because of its nature but rather that an unlimited tenure of life would be a wholly useless extravagance."⁴⁰ Nature follows her own course and is not deterred by death when the latter would serve some purpose.

Before entering upon the problem of death, particularly upon its causes and the associated phenomena of plant life, we shall briefly consider longevity among the various groups of plants and thereby

fill a noteworthy deficiency in botanical literature. There has never been such a compilation concerning the entire plant kingdom.

CRYPTOGAMS

ALGAE

Though the algae have been intensively investigated from various viewpoints and much has been contributed concerning their life histories, we have very little definite information respecting their longevity. Observations directed particularly upon this aspect are entirely lacking and I am able, consequently, to present only meagre information upon the subject, derived, for the most part, from Oltmanns.⁴¹

As is well known, the Laminariales include many genera of extraordinary size. The stalk of *Laminaria saccharina* attains a length of from 1 to $1\frac{1}{2}$ m. and that of *L. longirostris* may become as much as 5 m. in length; the spread of the former may be $2\frac{1}{2}$ to 3 m. and that of the latter 4 m. long and 60 cm. wide.⁴² Many species of *Lessonia* are tree-like in appearance and the stem of *L. fuscescens* becomes 3 to 4 m. long and thick as a man's leg. *Nereocystis* attains a total length of 100 m. and the stalk of *Macrocystis* may be as much as 200 m. in length. In its lower portion the stalk, secured to stones by its holdfast, is thick and destitute of leaves while the upper portions are rope-like and foliose. This astonishing length of *Macrocystis pyrifera* is all the more remarkable in view of the fact that these plants are of very primitive organization and belong to the algae. The tallest trees, by comparison, attain heights of 140 to 150 m. We may suppose in view of the colossal size of these algae that such plants do not complete their development within one year but require several years. I have been unable to find in the literature any information concerning the exact age of such algae. Oltmanns is in accord when he remarks that we are still uninformed concerning the age of large species among the Laminariales and that the only information which he found was a note by Foslie⁴³ stating that four to five years elapsed before a location, once denuded of its growth of Laminariales, was again colonized by specimens about one meter in height.⁴³ On the assumption that growth in length remains approximately the same during a long period of time and that this growth amounts to one meter every four years, a stalk of *Macrocystis pyrifera*, 100 to 200 m. long, must

be 100 to 200 years old.* Though this estimate may be only approximate it is, nevertheless, certain that this species of *Macrocystis* can attain an age which is common only among trees.

It is natural that the rings observable in cross-sections of stems in *Laminaria*, often 8 to 12 and more in number, should be regarded as annual rings. However, though their formation may be associated with changes in foliage or growth periods, there unfortunately is no good reason as yet for regarding them with certainty as annual rings. We can not employ them, therefore, for the determination of age.

In addition to those algae which live for years, there are numerous others which live for two years and finally an enormous number that exist for only one period of vegetative growth and which we can regard, though not entirely correctly, as annuals. Among them are many species which live for only a few weeks, as is indicated by their periodic occurrence and sudden appearance in great numbers and their equally sudden disappearance. These may be regarded as the shortest-lived among the algae.

Many algae can withstand unfavorable periods by various means, some the summer, others the winter. Among them, zygotes, oospores and other special cells assume the rôle played in this respect by seeds and bulbs among higher plants.

FUNGI

If we cover fresh moist horse-dung with a bell-glass, a dense moldy growth of *Mucor Mucedo* appears after a few days. Subsequent to formation of sporangia the fungus declines and in its place appears *Pilobolus crystallinus* which discharges its sporangia toward the glass wall, the source of light, and then also disappears in a few days. It is followed by a smaller mushroom, a species of *Coprinus*, which lasts for only a few weeks. Finally we observe a fungus of macroscopic size, often no larger than a pinhead, which belongs to the ascomycete *Ascobolus*. This rapid succession of fungal genera, suddenly appearing and then declining, indicates that very short-lived fungi which live for only a few days or weeks are involved. Do we not observe a similar situation in the woods? As though by a stroke of magic, a multitude of the most varied

*Though these figures appear inaccurate, they represent a correct translation of the original German.—E. H. F.

mushrooms (Agaricaceae, Hydnaceae, Clavariaceae) appears on the floor of the woods after abundant rain and warm weather and then disappears as quickly. They live for only a few days or weeks and the question arises as to how long the mycelium existed in the ground and supplied necessary materials for formation of fruiting bodies.

Thousands of microscopic multicellular fungi, occupying the greatest variety of places saprophytically or parasitically, rarely exceed one half to two years.

Many Myxomycetes, and Phycomycetes such as species of Chytridiaceae, Saprolegniaceae and Mucoraceae are short-lived and usually live, except for their spores, only a few weeks. There are also the parasitic Synchytriaceae, Cladochytriaceae, Peronosporaceae, Ustilaginaceae and Uredineae, and among these, particularly the Peronosporaceae and the rusts and smuts possess mycelia which live for months upon the host plants.

We are indebted to Jahn¹⁴ for noteworthy investigations on the longevity of plasmodia. His studies were concerned entirely with the plasmodium of the slime-fungus *Badhamia utricularis* Berk. This species grows very energetically and may easily be cultivated upon fungi which in Nature supply it with nourishment. In the dry atmosphere of a room it rapidly forms sclerotia and when deprived of food it soon sporulates. The longevity of the first cultivated plasmodium amounted to 77 days. Three other samples of the same strain lived 77, 71 and 76 days, respectively. There was an individual peculiarity of this material, however, for specimens secured from other sources could be kept alive 115, 145 and 150 days. Jahn noted two years and one month as the maximum longevity among his plasmodia.

Growth was generally vigorous at first, then gradually declined and finally ceased. This decreasing growth was not, however, the only indication of senescence. By employing plasmodia of various ages and allowing them to become moist again after first drying out, Jahn was able to make the interesting observation that young plasmodia readily resumed activity but that aged material did so with difficulty or not at all. Jahn remarks in this connection that the true curve of duration of latent life probably ascends rapidly at first and then descends slowly, suddenly falling off abruptly, and after a while continues to decline as a straight line. Jahn concluded

that the plasmodium suffered equally from loss of vitality whether in a dry or active condition.

These studies indicate that even in a simple organism as is represented by a slime-mold, youth, middle age and old age may be observed.

In the case of a long-lived plasmodium of about three and a half years, the youthful stage, *i.e.*, the period of energetic vitality and growth, lasts for about six months and is then followed by a critical period of decreased vitality and increased perishability. This is the behavior of the protoplasm under cultivation; in Nature the vegetative condition persists during the humid autumn probably no longer than four to six weeks.

Among the Ascomycetes are short- and long-lived species of *Ascoholus*, *Morchella* and *Peziza* which rapidly disappear when they have attained the fruiting stage; many Ascomycetes, on the contrary, overwinter, as in the case of *Rhytisma acerina* which produces the familiar black spots on maple leaves. Conidia develop during summer and Autumn which over-winter and not until spring do the ascocarps appear as the final stage on decaying leaves upon the ground.

The greatest longevity among fungi is to be found among woody and corky polypores which form large bracket-like fruiting bodies on trees and often require many years for their complete development.

The foregoing account indicates how incomplete our knowledge is concerning longevity of fungi and that it is impossible at present to present more exact details. I have found nothing particularly concerning longevity in mycological literature, not even in de Bary's¹⁵ well known work on the comparative morphology and biology of fungi and other plants, and this is equally true for lichens. Should such investigations be undertaken at some future time, attention must then be paid also to the various organs of fungi, for, though the pileus of the common edible mushroom and of other species may live for only a few weeks, the mycelium which remains in the substratum may behave altogether differently. It may resume activity again and again, dying off in its older parts. Attention must be paid to how long individual cells of the mycelium remain alive and it will probably be found that the mycelial cells

can attain a greater age in general than those of the fruiting body with the exception, of course, of spores.

Twenty-five years' experience with the unusual hyphae of mycelium N, as shown by their development in light, have indicated to me that this mycelium suffers in vitality within a year's time when kept under air-dry conditions and that the same is true also of *Xylaria Hypoxylon*.

Many fungi can survive long rest periods by means of sclerotia and other states of the mycelium. The duration of this period, as in the case of seeds, bulbs or root-stocks, varies individually and specifically according to conditions.

MOSSES

In all the bryological literature to which I have had access so far, I have found information concerning the age of mosses in only one study by Reichardt.¹⁶

In trees and shrubs the age of the stem may be determined anatomically, among other means, by the number of annual rings, and in the case of certain herbaceous plants, e.g., *Concavallaria polygonatum*, the age of the rhizome can be ascertained morphologically by the number of scars representing aerial shoots. Among mosses, however, there are no indications of age within the tiny stem and for this reason Reichardt attempted to establish the age of moss stems morphologically by vegetative relations and by the regular succession of axes. He came to the conclusion that we "can determine the age of moss stems in all those cases where there is a regular succession of axes of different rank, each of which indicates a region of annual growth." Otherwise, he says, the age of a moss stem can not be determined.

Since Bridel, two large groups of mosses have been recognized, the acrocarpic and the pleurocarpic. The acrocarpic are those whose main axis terminates in reproductive organs. They possess limited growth, therefore, and when they produce lateral branches, these, too, give rise to fruiting bodies at their ends and have, likewise, determinate growth. Production of reproductive organs occurs only once a year and the age of the stem may be determined according to the number of successive annual shoots.

The axes of pleurocarpic mosses, on the other hand, have indeterminate growth. Their reproductive organs do not arise on the

ends of the axes but laterally. Because of this, the age of such mosses can not as a rule be determined with certainty.

While referring to Reichardt's discussion in connection with those features which reveal the age of various mosses, I want to call attention to his remarks concerning determination of age in *Polytrichum*. He says that the way in which *Polytrichum* reveals its age is of the greatest interest and the only example of its kind. The male flowers of this plant form disc-like inflorescences on the apices of the stems. After flowering, the stem regularly grows through the inflorescence and extends beyond it. The next year it flowers again at its new apex and then develops on once more. On such a male plant of *Polytrichum* several disc-like inflorescences may be found one above the other, and since only one flowering disc appears annually these structures serve as a means of determining the age of the plant.

Finally, Reichardt concluded from his studies that the age varied in most cases between three and five years and that only in very vigorously growing stems was there six to ten years' growth.

I have found in species of *Polytrichum* that only the last one or two regions of annual growth were actually alive. When Reichardt speaks, then, of ages of three to five or six to ten years it must be understood that he found that many regions of annual growth on his plants though they may not all have been alive.

In figure 2 is portrayed a specimen of *Polytrichum* with five regions of annual growth, separated from one another by flowering discs.



FIG. 2. *Polytrichum* sp. Stem with 5 annual shoots separated by antherial discs. Original.

If we examine the stem of a moss plant from top to bottom we soon observe that the leaves suffer loss of freshness with age, turn brown, decay and finally disappear, leaving the stem denuded. The stem, too, eventually decays, though more slowly, and out of this progressive decay of leaf and stem from the bottom up there results an excellent layer of humus which makes thrifty growth for other plants possible. Among most mosses only a part of the stem is retained after it dies but in many others the entire dead stem persists. This latter condition occurs in two cases: 1) among peat mosses when their lower portions form a turf of peat; 2) when the lower parts of certain mosses become incrustated with calcium carbonate and gradually build up layers of tufa, sometimes several meters thick. Reichardt observed this latter process in the vicinity of the Neubans baths near Celje, Yugoslavia (formerly Cilli in Steiermark). The tufa was formed there by successive incrustations of the lower parts of a moss growing at its apex. So far as Reichardt was able to study the mass of tufa vertically, he found no interruption in the course of the stem. He arrived at the conclusion, therefore, that all the layers of tufa several meters thick were formed by gradual progressive incrustation in the lower parts of a turf which was growing at its surface.

Gymnostomum curvirostrum plays a great part in this incrustation and tufa formation and the extent of annual shoots can easily be determined. On the average, it is three lines. The elongation of this moss, therefore, amounts

In 4 years to 1 inch
In 48 years to 1 foot
In 288 years to 1 fathom
In 1440 years to 5 fathoms
In 2800 years to 10 fathoms

From his observations the author concludes that this and other species of moss can attain ages which vie with those of very old trees. Though Reichardt's investigations undoubtedly are of great value they do not, in my opinion, admit of the above-mentioned conclusion but only indicate that one and the same moss stem may repeatedly resume terminal growth for many successive centuries. When he says that mosses may become hundreds or thousands of years old he induces the misconception that the moss plant itself lives that long. That is certainly not the case, for only the upper

youngest one to ten annual shoots remain alive; all lower regions form a dense mass preserved by calcium carbonate. If we want to determine the actual age, *i.e.*, the time during which life is retained, we must consider only the last annual growth regions which are still alive. In the light of our knowledge so far no moss can live longer than ten years even under the most favorable conditions.

PTERIDOPHYTES

Ferns. Every transitional stage may be found from the delicate Hymenophyllaceae, only a few centimeters tall, to the mighty tree-ferns, 15 to 25 m. in height, and a great variety in age corresponds to this varied development in size. The mere sight of the palm-like stems of *Alsophila* and *Cyathea* with their umbrella-like crowns gives the impression that these plants represent relatively great age. From observations which I have made in the tropics on the growth of tree-ferns as well as from specimens of *Alsophila*, *Cyathea* and *Marattia*, cultivated in the palm-house of Schönbrunn in Vienna, I have come to the conclusion that tree-ferns can live for at least several decades.

Ferns exhibit perennial growth with either an above-ground or a subterranean stem. They live, accordingly, for two, or more, or for many years. The greatest age is to be found among the tree-ferns. An exact determination, even among the latter, is not possible, for there are no annual rings in the stems; the latter do not possess secondary growth and neither anatomical nor morphological criteria are available for the determination of age.

Most ferns produce spores either only occasionally or very often during their lives, and there are only a few which sporulate but once and then perish. Among the latter are *Ceratopteris thalictroides*, species of *Anogramma* as *A. leptophylla* and *A. chaerophylla*, and, among pteridophytes in the broader sense, *Salvinia natans*.⁴⁷

In the case of certain ferns, the prothallia can live during more than one period of vegetative growth, especially when for various reasons fertilization is suppressed. It appears to me very probable that the longevity of the prothallium can be considerably prolonged by prevention of fertilization through separation of male and female prothallia and it might also be possible to prolong the life

of the sporophyte by suppression of all spore-bearing fronds. Further investigation of this matter is very desirable.

The prothallium of *Gymnogramma leptophylla* can prolong its life and survive drying periods. It exhibits perennial growth* by means of adventive sprouting while the asexual generation, the fern plant itself, dies after spore formation.

Lycopodium. I have found by careful examination that the shoots of *L. annotinum* possess storied structure similar to that which has already been described for *Polytrichum*. The leaves of each year's growth project horizontally from the axis, from the base to a region near the apex, or they may be directed obliquely downward. At the apex of each year's growth they are smaller, however, and are directed upward into a small bud. These buds constitute rather distinct divisions between regions of successive growth and the number of annual shoots still provided with living leaves may be determined and thereby the longevity of the leaves themselves and of corresponding parts of the axes. One investigation of numerous individuals showed that under favorable conditions the stem was able to attain an age of from five to seven years.

PHANEROGAMS

Among flowering plants, except in the monocotyledons, the annual ring, which represents the yearly increase of wood, provides us with a generally reliable means for determining age. This is particularly true when the annual rings are sharply differentiated as in certain native trees, for example, the spruce, fir, pine, larch, oak, elm and false-acacia.

If, on the other hand, the annual ring is narrow, it often consists of but a few layers of cells and its thickness then is only a fraction of a millimeter. This is true of many trees in the far North where the ring count is difficult even with a lens and in some cases can not be determined any more accurately with a microscope. In addition, many tropical trees of equatorial regions, which live during the entire year under rather uniform meteorological conditions, show only very indistinct rings or none at all and render the count very difficult or impossible.

These circumstances have contributed not a little to the fact that we do not possess definite reliable information concerning the age of many trees and shrubs. Reports of age oftentimes are only esti-

mates and undoubtedly involve serious errors. It appears worthwhile, however, to assemble what is known concerning the age of phanerogams, so far as I have been able to gather from the very scattered literature, for such a compilation, though not entirely correct in many cases, is of importance in connection with the general question of longevity.

GYMNOSPERMS CONIFERAE

Sequoia. Among the longest-lived trees are the coniferous sequoias, characterized by their immense size. They were first discovered in 1850 by the English explorer Lobb⁵⁰ on the Sierra Nevada Mountains in California at an altitude of about 1500 m. There are two species, *S. gigantea* and *S. sempervirens*, both in California. They there form entire groves and the largest of the trees have been assigned various names by the settlers. Among these names are "Father and Mother of the Woods," "The Children," "The Three Sisters," "General Frémont" and "The Giant of the Woods."

These trees produce the redwood esteemed by the Americans and because of this they have been so wantonly felled that the American government decided to declare them a National Monument and thus save them from complete destruction.

In moist regions of Europe which are not too cold, as in the fertile valleys of Switzerland and near the Lake of Geneva, sequoias are planted very successfully as ornamental trees. Even in more northerly sections rather large trees may be found in wind protected and moist places. In the immediate neighborhood of Vienna, in Neuwaldegg, I found a fine tall specimen whose diameter at the base was about two feet, and while traveling in California in 1898 I did not fail to inspect these biological gigantic wonders near Santa Cruz. Since those trees are most worthy of being seen, excursions are organized in America for that purpose. From San Francisco one arrives at the station "Big Trees" in three and one-half hours by train and upon payment of a small entrance fee he enters a wood of *Sequoia gigantea*. Though I had already become acquainted with giant trees in the tropical forests of India and Java, I shall never forget the impression which these tree giants made upon me. One senses among them an astonishment akin to



FIG. 3. The Wawona Tree, *Sequoia gigantea*, in the Mariposa Grove of red-woods, California. Photo by U. S. Forest Service.

worship and thinks he has obtained a view into antediluvian times. Figures 3 and 4 give an approximate impression of the great dimensions of these mighty trees. One of them, known as General Frémont, rises straight as an arrow for about 100 m.; the lowest part of the bole is hollow so that ten persons can comfortably find room within the cavity. Close-by stands a still larger tree, taller and thicker with a circumference of 20 m. A horse and wagon can comfortably be driven through some of these hollowed trees. These are by no means the largest of the giants, however, for there are some which have attained a height of 142 m. and an age of several thousand years.

Sequoia gigantea produces trunks which on the average are 83 to 110 m. tall and 3 to 10 m. in diameter. One of these, "The Father of the Woods," was 142 m. tall and at the ground had a circumference of 36 m. One could enter its fallen trunk for a distance of 60 m. and emerge again through a knothole.

The British Museum in London possesses a cross-section of a tree with 1335 annual rings and the Museum of Natural History in New York has one of a tree which germinated in the year 550 A. D. At the Chicago exposition in 1893 there was on exhibit a cross-section which later was divided into parts and distributed among botanical collections. The Berlin Botanical Museum possesses one of these with a radius of 2.35 m. Careful counting showed 1316 annual rings. The circumference of this trunk was 28 m. at its base and its height is said to have been 112 m.⁵¹

Mayr⁵² also visited the sequoias during his journey through North America and established certain valuable facts, some of which will be presented here. Without attempting to find the biggest, he measured one in Fresno Co. and found it to be 102 m. tall. The green branches began at a height of 60 m. and the diameter, two meters above ground, was seven meters. Mayr did not think that trees 120 m. tall were in the least unlikely. On the basis of a dozen measurements of annual rings through the lower parts of several trees, he found that the average width of the annual ring was 1.2 mm. This number divided into the radius of the above-mentioned trunk gives an age of several thousand years. In the forestry museum of Brussels there is preserved a sector which measures 1.8 m. from pith to bark. It was derived, therefore, from a tree of only 3.6 m. diameter inside the bark; caring the



FIG. 4. The General Sherman Tree, *Sequoia gigantea*, in the Mariposa Grove of redwoods, California. Photo by U. S. Forest Service.

first decade the tree grew with annual rings 8 mm. wide; after the first 100 years the width of the annual rings amounted to 5 mm.; after 500 years to 2.5 mm. and after 1000 years to 1 mm.; at 1300 years their width was still 1 mm. The total age of the specimen was counted, not estimated, to be 1350 years. On the assumption that this growth was typical of all sequoias growing under similar conditions, he calculated the age of the most vigorous tree which he measured to be 4250 years and regarded that age as quite probable.

The findings of American investigators are in agreement with these figures, particularly those of Muir³³ who counted about 4000 annual rings on one trunk 10 m. thick and who estimated the age of other sequoias at 5000 years.

I am not in a position to judge whether the statements of other authors, who estimate the greatest height to be about 140 m. with an age as great as 6000 years, are justified, for accurate measurements are not available. However that may be, there is, nevertheless, no doubt on the basis of reliable observations that some trees may attain an age of about 4000 years and are thus the longest-lived organisms on our planet today.

Taxodium mexicanum Carr. Among the Taxodineae the Mexican swamp-cypress attains the greatest age and has long attracted attention by its great length of life. A specimen which Ferdinand Cortez is said to have regarded as one of the greatest wonders of America still stands in the little town of Tule in Mexico. The trunk, measuring more than 31 m. in circumference, one and a half meters above ground, supports a wide-spreading crown 35 m. high and so large that its circumference is about 160 m. A. P. De Candolle ascribed an age of 6000 years to this tree and A. von Humboldt attributed 4000 years to it. Comparative measurements have indicated, however, that this swamp-cypress can scarcely be more than 2000 years old,³⁴ further proof that estimates alone easily lead to inaccuracies and exaggerations.

Taxus baccata L. This species, formerly very common but now becoming scarce and even probably soon facing extinction, can attain great age. Mielek³⁵ calls attention to some very large and old yews, 900, 1225, 2096, 2600 and even 3000 years of age. According to the elder De Candolle, there are yew trees in England which were standing at the time of the introduction of Christianity.



FIG. 5. The great cypress of Tule. Courtesy of The New York Botanical Garden.

A thousand-year-old yew standing in Vienna is pictured in the well known work of Hempel and Wilhelm.⁵⁶ Its circumference at breast height is 3.07 m. and its height about 7 m.

A time-honored veteran is the yew at Fortingall in Scotland, whose circumference is recorded as being 52 to 56 ft. This tree was described as being cleft and hollow already in 1769. To-day it still consists only of two separate parts which stand in a semicircle while the upper portion is gone. The annual rings of the retained woody structure are very narrow, 35 per 2½ cm., and the tree's age is estimated at 3000 years.⁵⁷ In the cemetery at Crowhurst in Surrey are some yews whose age is estimated at 1500 years.

Evelyn⁵⁸ claims that in 1660 he was able to measure a yew tree in the cemetery of Braburn in Kent whose circumference amounted to almost 18 m. and which, according to A. P. De Candolle's calculations, was 2880 years old.

Faber⁵⁹ has presented a collective discussion of giant trees and of old trees in Europe. Among broad-leaved trees the wild chestnut becomes very old and is followed by the linden, elm, beech, poplar and walnut. Among conifers the yew, fir, spruce and larch become very large and old.

For various reasons we must employ caution in accepting reports concerning maximum ages. They are usually based upon approximate estimates and not upon counts of annual rings. It is well known that the yew possesses extraordinary sprouting powers, always appearing inclined to produce sprouts from dormant and secondary buds, especially when injured, a tendency which accounts for its great power of vegetative propagation. As Lowe⁶⁰ has pointed out, this tendency, as well as a method of forming trunks peculiar to this species, must be taken into account when judging the age of yew trees. All yews often form a false trunk composed of several stems and the former appears as though it were a single trunk; its age, consequently, may be far over-estimated. According to Lowe, the yew can attain an age of 200 to 250 years with a single trunk and allegedly older trees have false trunks. Whenever the intact trunk of a yew is shattered or damaged, which occurs at least once in a century, numerous shoots arise around the base of the main stem from adventive buds. On the way to Wyndcliffe, Lowe found a yew which, as is shown in figure 6, clearly exemplifies this development. Lowe says that this tree, 30 cm. in diameter

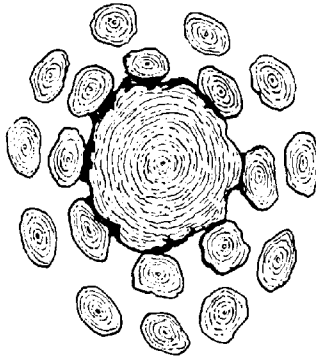


Fig. 6. Schematic section through an old yew at Tintern, England. Around the dead main trunk are two circles of daughter trees which presumably will all fuse together. From Lowe.

and about 60 to 70 years old, had already been dead 15 to 20 years but was surrounded by two circles of younger trees, 6 to 10 cm. in diameter. The eight small trees of the inner ring leaned directly against the dead trunk while the outer circle was composed of 11 trees somewhat smaller than those of the inner circle. The young trees stood so close to one another, however, that in the course of 50 to 60 years he expected them to grow together into a single trunk. The diameter of this trunk would then, according to customary calculations, indicate an age of about 400 years while actually it would be only 150 years old. The total diameter of the group at that time was 1.45 m.¹¹

***Cupressus sempervirens* L.** This tree, so strikingly characteristic of the Italian landscape, is native to northern Persia and the eastern Mediterranean region, having extended its territory progressively more and more eastward. It grows very slowly, attaining great dimensions and an age of 2000 to 3000 years.¹² Old trees are over 50 m. tall and up to 3 m. in diameter. "The old trunks in Giardino Gusti at Verona are famous; there are 200 of them, many of which are 400 to 500 years old and some of them reach a height of 40 m. Other well known specimens are the giant cypresses at the Villa d'Este at Tivoli near Rome, at the Alhambra in Spain and in burial grounds of Constantinople. Springer says there are sev-

eral cypresses around Lago Maggiore, 620 years old and 10 m. in circumference in the lower portions of their trunks. He states, furthermore, that a large specimen in Somma near Vesuvius had already become a stately tree in Caesar's time. Christ⁶³ mentions a tree 3.8 m. in circumference near Lugano and Grisebach⁶⁴ notes two others more than 1000 years old at the cloister of Lavra in Athos.^{193a, b}

Juniperus communis L. Freymann calls attention to the largest juniper in the parish of Ernus in Livonia, a tree which stood in the open near an old sacrificial site. Its circumference was $2\frac{3}{4}$ m. and its age estimated at 2000 years. Thirty years ago, after it had begun to dry out, the tree was broken by a storm.⁶⁵

Junipers 300 years old are more frequent. A specimen 48 mm. in diameter in the woods of the northern Taunus mountains was found to show 108 annual rings. A Norwegian specimen, 33 mm. thick, was 297 years old and another on the Kola peninsula, 8.3 cm. thick at the base, was 544 years old.⁶⁷

Juniperus nana Willd. An old specimen at an elevation of 2600 m. in the Alps was 103 years old.⁶⁸

Abies alba Mill. Nöggerath reported in his work of 1847 on the origin and development of the earth that a fossil coniferous trunk (fir?), 11 feet in diameter and with 792 annual rings, was found in the lignite deposits of Friesdorf near Bonn.

Mielek⁶⁹ describes firs 300, 400 and 500 years old. According to Wilhelm,⁷⁰ these trees can become 1.5 m. thick and 200 to 400 years old. Other figures ascribe ages even as great as 800 years⁷¹ and Schacht counted 350 to 700 annual rings.⁷²

Picea excelsa Lk. The maximum ages of Norway spruce are reported as being 200, 300, 400 and even 1200⁷³ years.

The so-called "Monkey Valley spruce" at Eichstätt in Bavaria has a circumference of 6.3 m. around the stump, 5.3 m. at breast height and a total height of 38 m. An estimate of its annual rings indicates an age of 350 to 400 years.

The spruce of Stiegelschwand in the Canton of Bern is estimated at 300 to 400⁷⁴ years.

Larix decidua Mill. Trunks 35 m. and more in height with diameters of $\frac{3}{4}$ m. are known and can attain an age of more than half a century.⁷⁵

In Wallis, especially in the Park of Saas-Fee, are the slow-grow-



Fig. 1. Base of a 3000-year-old juniper. Cache National Forest, Utah. Photo by U.S. Forest Service.

ing larches of the high mountain ranges. They are known as stone or ridge larches and are healthy trees, one to one and a half meters thick and 600 to 700 years old.

Klein⁷³ counted the rings of such trees to determine their age. Trees of similar size, though isolated, occur in the neighborhood of the Riffelalp where, according to Klein, "a sawed-off larch stump near the Findel glacier, 85 cm. thick within the bark at breast height, showed 20 narrow rings in the innermost part, then about 100 wide ones and finally narrow ones again, altogether 417 rings."

The maximum height of the larch has been reported at 53.7 m., the maximum diameter at 1.6 m. and the greatest age at 600 years.⁷⁶

Pinus sylvestris L. Böhmerle⁷⁷ reports 584 years as the greatest known age limit of this species. Various other Scotch pines are recorded as being 150, 250, 300, 463 and 500 years old.

Pinus nigra Arnold var. *austriaca* Höss becomes 500 to 600 years old.^{78a-c}

Pinus canariensis C. Smith attains an age of 440⁷⁹ years on Teneriffe, according to Schacht.

Pinus Cembra L. According to Klein's⁸⁰ views, the alleged maximum age of the Swiss stone-pine is usually too low. According to Kerner and Willkomm, it amounts to 700 years. Woditschka estimates the age at 500 to 600 years, in some cases at 1000 years. Klein was in the fortunate position of being able to make exact determinations in this direction, for he discovered specimens of wonderfully developed and very old stone-pines on stony slopes by the Findel glacier in the neighborhood of the Riffelalp. Included was a tree with the very unusual circumference of 7.65 m. Klein explains his method of determining the age of this specimen as follows. In the immediate vicinity of this tree were several very old pines sawed off about one meter above the ground. The wood of these stumps was so sound and well preserved that their ages could be accurately determined by ring count to within two or three decades. The average diameters and ring counts corresponded so well among these stumps that the true age of the largest pine could be calculated on the basis of its circumference. Of the three stumps which he examined the largest had a circumference of 4.8 m. and a diameter of about 1.53 m.; approximately 730 rings could be counted to which 20 more had to be added for the small decayed portion in the center, giving a total of 750 years. A second



FIG. 8. The remains of a 1000-1100-year-old Swiss stone pine, the oldest in Switzerland. Circumference 7.67 meters. Sept. 6, 1899. From Klein.

stump, 2.3 m. in circumference and 73 cm. through, had 340 rings; a third, 1.7 m. around and 54 cm. thick, showed 250 rings, and a sawed-off branch of the big pine, about 50 cm. through, likewise showed 250 rings.

One observes in these figures that the age is about five times the diameter expressed in centimeters. Multiplication of the above diameters by five gives, then, 765, 365, 270 and 250 years. For our purpose, these figures based on diameters agree completely with those determined by actual count of annual rings. If we multiply the diameter of the largest pine, 243 cm., by five, we arrive at the extraordinary figure of 1215, in round numbers, 1200 years as the age of our tree.

Another pine observed by Klein on the same site had a circumference of 4.58 m. Klein estimated its age to be between 1000 and 1200 years and it might have been even older.

Pinus Strobus L. Specimens 400 to 450 years and older are known.⁸¹

Dammara australis Steud. According to estimates of Hochstetter, there are specimens of Kauri pine 700 to 800 years of age.⁸²

Cedrus Libani Loud. According to Booth who traveled on Mount Lebanon in 1836, there were still about 350 specimens of this species. "The youngest of them," he says, "was about 25 years old and the oldest appeared so old, in view of its unusual dimensions and antique aspect, that it would not be at all surprising if these trees already existed at the time of Solomon."⁸³ The largest tree had a circumference of about 46 feet 8 inches and was 110 feet tall.

The age of the oldest of these trees can not be determined more precisely because it is hollow and only the bark and a narrow portion of the wood remain. According to various observations,⁸⁴ including those on the growth of the oldest cedar in the Jardin des Plantes in Paris, this species can acquire an age of 1200 to 1300 years.

GNETACEAE

Welwitschia mirabilis Hook. f. A member of the Gnetaceae, very remarkable because of its structure, whose short stem 60 cm. tall bears, in addition to two cotyledons, only two large, opposite and persistent, thick, leathery leaves up to about one and a half meters wide and two meters long. Entire at first, the leaves later become frayed their entire length into several contorted and upwardly arched

ribbons, their tips lying on the ground. At the base of the plant is a region which periodically elongates. From this region the leaf continues to develop, while at its tip it gradually dries out and dies off. The plant grows very slowly and becomes 70 to 100 years old.⁵⁴

ANGIOSPERMS

Monocotyledons

Definite information concerning the age of long-lived monocotyledons is not available because the stems of these plants do not possess annual rings and we have, consequently, no reliable means of determining their ages. The attempt to decipher their ages by means of leaf scars likewise leads to no practical results.

We must conclude, however, from the stately proportions which palms can acquire, that they are indeed able to attain great age. The wax palm, *Ceroxylon andicolum*, which grows in the Andes and which was carefully studied by A. von Humboldt, exhibits heights of 52 to 60 m. Concerning its age, however, the literature contains no reliable information.

LILIACEAE

***Dracaena Draco* L.** When the Spaniards captured the island of Tenerife in 1492, they found a large dragon-blood tree in the town of Orotava, which then already was very old. A. von Humboldt admired the same veteran in 1799 and estimated its age to be between 5000 and 6000 years. Its circumference at that time was about 15 m. and its height approximately 22 m. As is indicated in figure 9, the trunk had a huge cavity which gradually weakened it to such an extent that in 1868 it was destroyed by a hurricane.⁵⁵ On the basis of these historical facts and the idea that the dragon tree grows very slowly, Humboldt regarded this tree as very old and estimated it to be 6000 years of age. That was merely an estimate, however, for the dragon tree is a monocotyledonous plant whose age cannot be accurately established because it possesses no annual rings.

A few years ago Pütter^{56a, b} spent some time on Tenerife and made a most valuable critical study of the age of the dragon tree. He rejected, first of all, the historical basis which Humboldt employed, because little credit could be accorded the numerous tales of the inhabitants who not infrequently do not know their own ages or



FIG. 9. The alleged 6000-year-old dragon-blood tree, *Dracaena Draco*, of Orotava, Teneriffe. From the original drawing by J. Selleny.

that of their children. Pütter endeavored, therefore, to determine whether the dragon tree really grows so very slowly, and because Humboldt's tree no longer existed he sought comparable but living specimens. It developed that in 1799 the tree of Orotava possessed a circumference in the region of its roots of 14.6 m.; a diameter, 2.8 to 3 m. above ground, of 3.3 to 3.65 m.; and a height of between 15 and 18 m. The tree of Icod de los Vinos in 1925 was 17.45 m. around near the root, 4.82 m. in diameter and 22 m. tall.

These measurements indicate that the tree of Icod exceeds the one observed by von Humboldt in all dimensions. According to the measurements of Schacht, Samler-Brown, and Pütter, the tree of Icod has annually increased 8 cm. in circumference during the last 68 years. On the basis of Pütter's calculations, we can conclude that the dragon tree of Icod, which surpasses the famous



FIG. 10. The dragon-blood tree of Icod de los Vinos, about 22 meters tall in 1923. From Pütter.

Humboldt tree in size, is certainly no older than 185 years. According to Pütter, the peculiar method of branching which the dragon tree exhibits can also be used as a criterion of its age. As soon as a shoot has bloomed it thereby loses its terminal growing point; thereupon elongation takes place and new shoots arise beneath the old tips. The dragon tree usually blooms every 8, 11 or 12 years. If this is correct we should be able to determine its size on the basis of the number of flowering periods as betrayed by the scars. By this means also Pütter became convinced that among the living dragon trees none was more than 200 years old. He regarded the tree of Icod as being 160 to 170 years of age, and since this tree is larger in all its dimensions than the famous one of von Humboldt there is reason to doubt that the latter was any older.

Dracaena cinnabari Balf. fil. Prof. O. Simony, who traveled through Socotra⁸⁷ in the service of the Imperial Academy of Sciences in Vienna, brought, among other things, a photograph of an old specimen of *Dracaena cinnabari* whose diameter was 1.6 m. According to these dimensions, we must conclude that this tree, too, can attain a great age.

Polygonatum. The subterranean parts of this genus permit determination of its age according to the large scars which remain on it after the dying-off of the aerial shoots. It is these scars which have bestowed upon the plant the name of Solomon's seal. The plant consists of a fleshy, creeping, sympodial axis with very distinct internodes which are separated from one another by the already mentioned scars. Since the internode represents the annual growth of the rhizome, the age of the entire living rhizome and of each part thereof can be determined by the number of internodes or scars. The root-stock grows at its tip and dies off behind. The individual annual increments long remain alive, at least for 15

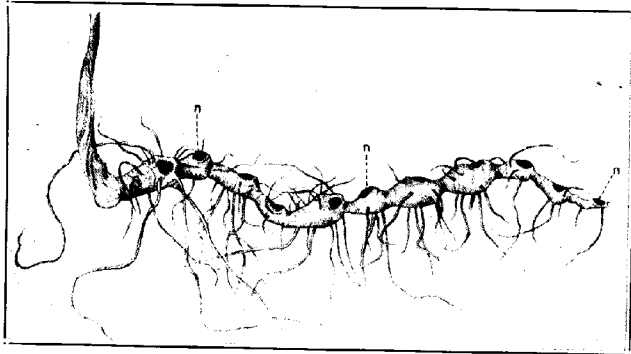


FIG. 11. *Polygonatum officinale*. A rhizome with eleven leaf scars indicating as many years of growth. Original.

years. Such 15-year-old axes in the case of *Polygonatum multiflorum* can become more than 40 cm. long.⁸⁸

Upon my instigation, Flamm⁸⁹ investigated the age of the rhizome of several species and found that the following ages can be attained:

| | |
|--|---------|
| <i>Anemone ranunculoides</i> | 7 years |
| <i>Polygonatum latifolium</i> | 8 " |
| <i>Asarum europaeum</i> | 14 " |
| <i>Polygonatum officinale</i> | 16 " |
| <i>Polygonatum multiflorum</i> | 17 " |
| <i>Polygonatum verticillatum</i> | 17 " |
| <i>Anthriscum ramosum</i> | 17 " |
| <i>Paris quadrifolia</i> | 17 " |

DICOTYLEDONS

BETULACEAE

Betula verrucosa Ehrh. Greatest age usually 90 to 100 years; rarely 120 years or more.^{20a, b}

Betula nana L. We are indebted to Kraus²¹ for valuable data concerning the longevity and growth of some northern shrubs including, among others, the dwarf birch, figures concerning which are presented in the following table.

AGE AND GROWTH OF THE DWARF BIRCH AT 73°4' N. LAT.

| No. | Age | Radius of stem in mm. | Width of annual ring in mm. | Remarks |
|-----|-----|-----------------------|-----------------------------|---|
| 1 | 40 | 4 | .1 | Eccentric growth, thick as a quill, about 1 dm. long; much-branched stem with corresponding root development. Maximum radius, 4 mm.; minimum, 3 mm. |
| 2 | 80 | 6 | .07 | Very uniformly developed. |
| 3 | 53 | 12 | .23 | Well developed round stem. |
| 4 | 67 | 8.5 | .13 | Diameter 12 mm. |
| 5 | 62 | 9 | .14 | Root. |
| 6 | 10 | 16 | 1.6 | A specimen from the Botanical Garden of Würzburg. |

This table indicates that the oldest tree investigated was 80 years of age although the radius of its stem amounted to only 6 mm. This is understandable if we take into consideration its extraordinarily narrow annual increments in diameter, for the thickness of the annual rings was only .07 mm. Such plants of the far North appear young at first sight but upon closer examination they show up to be old and crippled veterans which attain great age in spite of the unfavorable conditions of the Arctic.

Since flowering, fruiting and reproduction of northern plants often suffer from climatic factors, special adaptations provide for

the maintenance of the individuals and they are thereby assured the greatest possible longevity.⁹² This is equally true of other woody plants of eastern Greenland investigated by Kraus and to which I shall later refer, *viz.*, *Salix arctica* Pall., *Vaccinium uliginosum* L. and *Dryas octopetala* L.

Plants growing in mild climates attain in their youth greater thickness than do those of the Arctic. This is exemplified in the oldest specimen of dwarf birch from the Schongauer moor, which revealed only 22 annual rings in a diameter of 1 1/3 cm.⁹³

Betula odorata Bechst. from the Kola peninsula showed 124 rings in a 22 cm. cross-section.⁹⁴

Alnus glutinosa Gaertn. 100 to 120 years old, though one specimen has been estimated to be 300 years of age.⁹⁵

Alnus incana Moench. A specimen on the Kola peninsula had a diameter of 48 cm. It must have been rather old if we reflect that a sector of another trunk in the same region showed 63 annual rings.

Carpinus betulus L. The hornbeam seldom acquires an age greater than 150 years though in isolated cases it may exceed 250 years.

Carpinus duinensis Scopoli. The oriental hornbeam seldom exceeds 100 years.

Ostrya vulgaris Willd. Seldom exceeds 100 years.

Corylus avellana L. 60 to 80 years. A giant specimen in the park of the Schwöbber estate in Hanover is estimated at 150 years.⁹⁶ It is 10 m. tall and 2.2 m. in circumference, 1 m. above the ground.

Corylus colurna L. Generally not over 100 years.

Castanea vulgaris Lam. The chestnut becomes very old, 200 to 500 years of age. The famous Castagno dei Cento Cavalli on Mount Aetna is worthy of mention. Within the memory of man, its trunk has always been hollow and divided into five sections with a total circumference of 64 m. Kanngiesser refers to the idea that these five sections once formed a single tree and Swinburne claims to have become convinced by digging around the tree that although it is split to the ground the five sections are all united underground.⁹⁷ On the Donnersberg in the Rheinpfalz there stands a 400-year old trunk 9 m. in circumference and in the Maggiatal is a 500-year old specimen.

FAGACEAE

Fagus sylvatica L. Seldom exceeds 250 years.⁹⁸ In exceptional cases there are older specimens. One of the largest stands at Montigny (Seine-Inférieure) at the edge of the wood Roumare. Its age is calculated to be between 600 and 900 years.^{99a, c}

Kanngiesser¹⁰⁰ gives a list of very old trees in a table which is presented herewith. Obviously, only those specimens are considered which possess a circumference of more than five meters.

FAMOUS OLD BEECH TREES

| Location | Circumference in meters | Height of diameter determination | Estimation of age in years |
|---|-------------------------|----------------------------------|----------------------------|
| Beech at Flims in Graubünden ¹⁰¹ | 5.30 | 1.20 m. | 300 |
| Ludwig's beech in the Oberförsterei of Kranichstein near Darmstadt ¹⁰² | 5.30 | Breast-height | 300 |
| La Houssaye, near Guerbaville, Normandy ¹⁰³ | 5.43 | 1 m. | 375-575 |
| Le Bourdigale beeches near Haye, Normandy ¹⁰⁴ | 5.55 | 1 m. | 375-575 |
| Widenberg in Oberfranken ¹⁰⁵ | ca. 5.8 | | 800? |
| Burghof beeches near Jena in the vicinity of the forest house ¹⁰⁶ | 2.70 | 1 m. | 100 |
| High beeches at Dannweiler, Rheinpfalz ¹⁰⁷ | 6.30 | 1 m. | - |
| At Dänisch Neuho ¹⁰⁸ | 7.40 | 30 cm. | - |
| Montigny, Normandy ¹⁰⁹ | 8.20 | 1 m. | 630-930 |
| Neuhüttengraben in mts. near Tegernsee ¹¹⁰ | 7 | Breast-height | - |

Quercus pedunculata Ehr. The English oak¹¹¹ can become very old but its age is often over-estimated, for on favorable soil it can grow 1½ m. in diameter and yet be not more than 125 years of age. Three-hundred-year-old oaks are not a rarity in Spessart. Five-hundred-year-old trees have also been found and Kanngiesser and Mielck admit even 1000 years.

The well known botanist, Goeppert, together with his students, used to visit one of the largest oaks of Germany, an English oak which stood at Pleischwitz near Breslau. In 1846 this tree was more than 24 m. tall and had a diameter of 4.4 m. and a circumfer-

ence of 13.2 m., two thirds of a meter above ground. Its trunk was hollow and the cavity could accommodate 30 men. When this tree broke down in 1857 its age could be determined fairly accurately and was found to be 700 years. Since this was one of the largest oaks known, we may conclude that oaks can only rarely attain an age of 1000 years or more, for even the largest of those described by Evelyn¹¹² were not so great as the Silesian giant. Likewise the oak described by von Humboldt which stood at Montravail near Saintes in the Charante Inférieure and whose age was regarded by him to be between 1800 and 2000 years, could hardly have been half so old. This is indicated by a French record¹¹³ which states that it was only 10.85 m. in circumference, one meter above the ground, smaller dimensions than those shown by the 700-year-old oak of Pleischwitz.

At the gate of the water-way at Magdalen College at Oxford there was an oak so large that it could shelter 3000 persons. Severely mistreated during the construction of a walk, it was destroyed in 1788 and its age was calculated at 900 years.¹¹⁴

According to Becker,¹¹⁵ the average age of the oldest oaks in Hasbruch should be estimated at 1200 to 2000 years, and on fallen trees 1100 and 1500 annual rings were counted without taking into consideration the central cavity. The diameter of the largest tree was 2½ to 3 m. at breast height.

Joly¹¹⁶ reports an old oak at Erle in Westphalia whose circumference at breast height was 12 m. and whose age was estimated at 1500 years.

The following table derived from Kanngiesser¹¹⁷ concerns various famous old oaks. It is not always clear, however, which species is concerned. The English oak, *Q. pedunculata*, becomes much older than the Durmast oak, *Q. sessiliflora*, and, therefore, very old specimens must be regarded in most cases as being English oaks. It is Kanngiesser's opinion that those greater than 10 m. in circumference are, probably without exception, English oaks.

Kanngiesser¹¹⁸ gives valuable details concerning the oaks mentioned in this table.

Quercus sessiliflora Salisb. An oak on the estate of Imbshausen in Hanover had a circumference of 8.5 m. at breast height and, close to the ground, 10.5 m., while its age was estimated at 600 to 700 years.¹⁴⁰

Quercus Cerris L. Usually not over 100 years.
Quercus Ilex L. Can become several centuries old.

FAMOUS OLD OAKS

| Location | Circumference in meters | Height of diameter determination | Estimation of age in years |
|---|---|---|----------------------------|
| Greendale Oak in Walbeck Park ¹¹⁸ | 9.30 (1903) 10.20 (1664) 11.10 (1790) | Breast-height At the ground " " " | - - - |
| Erzherzog-Johann-Oak ¹¹⁹ (dead and without bark) | 7.98 | Breast-height | 500-600 |
| Royal Oak, Windsor ¹²⁰ | 8 | 93 cm. | 1200* |
| Fingerpost Oak at Eisolzried ¹²¹ | 8 9 | Man's height 3 m. | 700 |
| Schönberg Oak at Kempton ¹²² | 8.50 | Breast-height | - |
| Broad Oak at Kirtori ¹²³ | 7.90 | " | 800-900 |
| At Belmesnil in Normandy ¹²⁴ | 8.85 | 1 m. | 700-900 |
| Broad Oak at Bruckmühl ¹²⁵ | 10.20 | 30 cm. | 1000 |
| Devil Oak at Volkenroda ¹²⁶ | 9 | 63 cm. | - |
| King Max Oak at Kirchseon ¹²⁷ | 9 | Breast-height | - |
| Chapel Oak at Allouville ¹²⁸ | 9.79 | 1 m. | 800-900 |
| Owen-Clendower Oak at Shrewsbury ¹²⁹ | 12.50 | - | Standing already in 1403 |
| Mayors-Oak at Worksop ¹³⁰ | 10.5 | 1.55 m. | - |
| Wendelin-Oak at Geisfeld ¹³¹ | 9 | 2.5 | 1100 |
| At Pleischwitz in Silesia, overthrown by storm in 1857 ¹³² | 13 | 63 cm. | 700-800 |
| Montravail at Saintes ¹³³ | 14.10 | At the ground | 2000? |
| Fairlop Oak in Essex ¹³⁴ | 14.88 | - | 500? |
| At Körtlinghausen in Prussia ¹³⁵ | 12.4 | Near the ground | - |
| Cowthorpe Oak at Wetherby in England ¹³⁶ | 16.8 13.5 11.5 | At the ground 92 cm. 1.65 | 1500 |
| At Wehlau in East Prussia, no longer standing ¹³⁷ | 18 | - | - |
| Danorey Oak in Dorsetshire, overthrown by storm in 1783 | 21 | - | - |
| St. Joseph Chapel Oak at Villedieu in France ¹³⁸ | 19.08 12.29 | At the base 1 m. | - |

JUGLANDACEAE

Juglans regia L. The maximum age, according to Willkomm, is between 300 and 400 years. The big walnut in Beckenried was

supposed to be 400 years old, while many others are thought to have attained an age of 900 years. These figures are only estimates, however, and may be exaggerated because one of the oldest of the known giant specimens in Interlaken was only about 160 years of age. It is Parmentier's opinion that the walnut usually begins to decline at 120 years.¹⁴¹

SALICACEAE

Salix alba L. Kanngiesser refers to several very old silver willows, one of which in Weizendorf near Rastenburg was 7 m. around and was estimated to be at least 150 years old.

Salix fragilis L. The same author mentions an old crack willow 140 years of age.¹⁴²

Salix arctica Pall. Among several trunks on the island of Sabina which were investigated by Kraus, there was one whose radius amounted to 31 mm. and whose annual rings indicated an age of 150 to 200 years.¹⁴³

Salix myrsinites L. One trunk, 6.5 cm. in diameter, showed 99 annual rings (Kanngiesser, according to Kihlmann).

Populus alba L. Silver poplars, 300 to 400 years old, are not exactly rare. One of the largest in Leipheim in Schwabia was 12 m. in circumference about 30 cm. above the ground; one meter above ground it was 11 m. around and the age of the tree was about 600 years.¹⁴⁴

Populus nigra L. This species, too, can become several centuries old. In the Botanical Garden of Breslau, not far from Kaiser Friedrich place, stands a tree, 8 m. in circumference at a height of 1½ m.,¹⁴⁵ whose age is estimated at 300 years.¹⁴⁶

A gigantic hollow specimen of *Populus nigra* stands in the Botanical Garden of Dijon in France. It is 40 m. tall, 14 m. in circumference near the ground and its age is estimated, by comparison with neighboring trees, to be at least 500 years.¹⁴⁷

Populus tremula L. The largest recorded trembling aspen stands in Aastrup near Hadersleben. It is 21 m. tall and 3.73 m. around, 1.3 m. above the ground, and presumably is 140 to 150 years old.

URTICACEAE

Ficus religiosa L. According to various descriptions by travelers as well as my own observations in the tropics, it is certain that the

various arborescent species of fig can attain great age. The exact measurements I have not been able to find. Relatively accurate data, though not by scientific people, concern that famous *Ficus religiosa* which stands near Anuradhapura in the northern part of the former Kingdom of Kandy (Ceylon) and under whose crown Buddha is supposed to have rested. In his work upon Ceylon which appeared in London in 1859, J. E. Tennent ventures the opinion that the sacred tree, so far as records reveal, is the oldest tree in the world since it was already planted in 288 B. C. and must, accordingly, have attained an age of 2147 years. The tree is held sacred and kings dedicate their possessions to it in the thought that beneath it Buddha rested at the time of his apotheosis. No weapon may injure the tree and no leaf of it may be plucked; only those which have fallen may be gathered and distributed among the faithful as sacred tokens. The tree has been revered for 2000 years and, since this reverence has never ceased but extraordinary care has been accorded it, Tennent regards it as unlikely that the original tree has ever died and been replaced by another.¹⁴⁸ This old fig tree is mentioned also in Ritter's Geography (IV, 2, pp. 237, 251, 681), in Lassen's Indian Archæology (I, p. 260) and in the voyage of the Austrian frigate "Novara" (p. 288). The zoologist Schmarda also saw it but remarked that the tree was not impressive in either form or size and that it resembled in his opinion our white poplar.¹⁴⁹

Heber¹⁵⁰ mentions a giant fig on the island in the Rerbudda river belonging to the Residency of Bombay. It was standing when the Portuguese first landed in the East Indies and investigations of Englishmen have shown that it is not unlikely that Nearchus, companion of Alexander the Great, saw and marveled at this tree, to which an age of about 3000 years can therefore be attributed.¹⁵¹ In any event, it is certain from old reports and from the extraordinary dimensions which figs can attain that they are among the longest-lived plants known.

Ulmus. Whenever old elms are mentioned in the literature their specific names unfortunately are not given and we do not know which species are concerned. According to a record in the town of Morges in Switzerland, dated May 10, 1824, an elm of unusual size was destroyed in the park of that city.¹⁵² It possessed a height of 36 m. and a circumference of 16.68 m. beneath the first branch;

3.6 m. above ground it was still 10.29 m. in circumference. The stump showed 335 annual rings.

The age of another elm which stands in the public square of Schimsheim and whose circumference was more than 13 m. one meter above ground, possesses an estimated age of 600 years.¹⁵³

Oxford has the famous elms, *Ulmus campestris*, of the "Broad-walk" at Christ Church College. They extend back to the time of Charles I and may have been planted between 1630 and 1640. "Of the 75 trees which once stood on each side of the walk 60 are still alive, none of which is entirely intact."¹⁵⁴ Therefore, the elms of England are usually not more than 300 years of age.

The largest specimen of *Ulmus effusa* so far described stands in the garden of the Perkan estate. Its circumference at a height of 1.3 m. was 6.43 m. in 1908, at which time it was 20 m. tall and 300 to 400 years old.

Celtis australis L. Becomes several centuries old.

PLATANACEAE

Platanus. The ancients were impressed by the gigantic growth of the sycamore, which they held in high esteem.

Pliny spoke of a sycamore in Lycene in whose hollowed trunk the consul Metianus was able to spend the night with 18 companions.

Pausanias tells about a giant sycamore which stood in Arcadia by a spring at Caphiae and which was supposed to be 1300 years old.

Particular fame is attached to the large group of sycamores in the village of Bujukdere on the Bosphorus near Constantinople. This group now consists of seven trees¹⁵⁵ and De Candolle the elder gives the circumference of the largest trunk as 150 feet and that of its cavity as 89 feet. No acceptable information is available concerning the age of this hoary giant.

BUXACEAE

Buxus sempervirens L. Röhrig¹⁵⁶ estimates the age of a hedge in the garden of the chief forester of Hachenberg at several hundred years. The hedge was 1.6 m. tall and equally wide. According to Kanngiesser,¹⁵⁷ however, these plants can not attain more than 150 years of age.

CACTACEAE

Carnegiea gigantea Britton & Rose. This giant cactus of the sub-tropical zone of the North American flora forms stems which under favorable conditions attain a height of 18 m. and a diameter of 60 cm.¹⁵⁸ Certainly an extraordinary size when one considers that in these plants we are dealing, not with a tree in the true sense of the term, but with a very succulent and relatively weak stem of a cactus. In youth the simple stem is erect, cylindrical, many-ribbed and thickly beset with formidable thorns. Later in life it usually develops erect and whirled side branches in a chandelier-like fashion. When old, the upper portion of the stem decays and leaves the tough isolated vascular strands as individual rods which are united into a single solid cylinder.¹⁵⁹

LAURACEAE

Laurus nobilis L. As may readily be observed about the Italian Lakes, the laurel can attain great size, and near Lake Lugano is a tree 1.56 m. in circumference. According to Hempel and Wilhelm,¹⁶⁰ the laurel attains a height of 15 m. and a width of 25 cm. during 20 years continual growth. Only the scantiest of data are available concerning age, however, and the laurel of Syra which Pausanias mentions is represented as being one of the oldest trees of the known world of his time.¹⁶¹

BERBERIDACEAE

Berberis vulgaris L. Kanngiesser found a 24-year-old tree.¹⁶²

Clematis vitalba L. Kanngiesser notes a stock 24 years old whose root-stock was 41 years of age.

MAGNOLIACEAE

Magnolia acuminata L. A specimen on the estate of Benkhäusen was shown to be 100 years old.

CISTACEAE

Helianthemum canum Baumg. Though its shoots usually do not exceed 15 cm. in length, this species, nevertheless, attains relatively great age. The oldest and incidentally the largest specimen showed 28 annual rings through the root-crown.

BOMBACACEAE

Adansonia digitata L. Just as the big-trees by their age and size convey the impression of majesty, even of sublimity, so do the



FIG. 12. A giant cactus, *Carnegiea gigantea*, Tonto National Forest, Arizona.
Photo by U. S. Forest Service.

baobab or monkey-bread trees.¹⁶² These colossals of Africa with their huge trunks appear like gigantic relics of a past age.

At the mouth of the Senegal, Adanson found an unusually old specimen, the diameter of whose trunk amounted to 10 m. He regarded it as the oldest tree on earth and by comparison of diameter growths among various individuals he calculated its age at 5150 years. According to Schacht's reckoning, however, the annual diameter increase of the trunk appears under-estimated and the age, consequently, over-estimated. Even though Adanson's figures may be exaggerated, there can be no doubt that the monkey-bread tree can attain great age. On several large trunks Adanson observed that the names of French and Dutch sailors had been inscribed in letters 16 cm. tall, together with dates of the fourteenth and fifteenth centuries.¹⁶³ The hollowed trunks of these giants serve as dwellings and storage places for the negroes and also for tribal meetings.

TILIACEAE

Tilia. Lithuania is famed for its old lindens and in that country stands the largest specimen yet measured. Its circumference was 25.7 m. and the annual rings betrayed an age of 815 years.

One of the oldest, a specimen of *Tilia platyphyllos*, stands in Neuenstadt on the Kocher¹⁶⁴ in Württemberg. According to a record preserved in the city archives of Stuttgart, this linden must have been a large tree already in 1448. In 1881 the circumference of this tree, which now stands as an old ruin, was about 14.5 m. and its age was reckoned at 700 years.

Kanngiesser¹⁶⁵ gives detailed accounts concerning the linden of Staffelstein, famed for its age and size, which at its base was 16.5 m. around and 4.5 m. through. Held together by iron bands, it, too, now resembles a ruin. The age of this linden, supposed to be *Tilia platyphyllos*, is estimated at 800 to 1000 years.

ACERACEAE

Acer campestre L. One of the oldest specimens of this species is located in the southern part of the castle park at Oberglogau. Its circumference is 3.4 m., 1.25 m. above the ground, and it is estimated to be between 150 and 200 years of age. This species rarely becomes more than a century old.

Acer platanoides L. A veteran of this species stands in the

chief forester's district of Lautenthal in Hanover. It is 25 m. tall and 5.1 m. in circumference, one meter above ground, and is supposed to be 400 to 500 years old. Trees of this species more than 150 years of age are rare.

Acer pseudoplatanus L. One of the largest trees of this species stands near Kern in the Melch valley of Switzerland. Its circumference is 12.2 m.¹⁶⁶

Acer montanum Ait. becomes upward of 200 years of age.

AQUIFOLIACEAE

Ilex Aquifolium L. The common holly can become several centuries old. One of the largest, perhaps the oldest, stands on the estate of Gourdiehill in Perthshire. Its circumference is 2.21 m. at the ground and $1\frac{1}{2}$ m. higher it is still 1.98 m. around and maintains this size up to a height of 9 m. where the first branch is located.

RHAMNACEAE

Rhamnus cathartica L. Willkomm claims that the buckthorn can become more than 100 years old.

Rhamnus Frangula L. The oldest glossy buckthorn in Marburg showed 30 annual rings.

VITACEAE

Vitis vinifera L. In a conservatory of Kinnell near Auchmore a stock has been raised for about 50 years whose length is approximately 50 m. I knew of a wild stock in Vienna very close to the Heustadlwasser near the main road which possessed a circumference of 55 cm., one half meter above ground, and an estimated age of 80 to 100 years. In America, particularly in the forests along the Mississippi and Missouri rivers, the vine attains extraordinary size, producing, it is said, stems one foot in diameter and 100 feet tall.

ROSACEAE

Ribes rubrum L. Stems 4 to 11 years old are known.

Rosa. Though the upper shoots of the rose do not become old the entire plant can, nevertheless, attain considerable age, for it continually grows by underground stem and root shoots. Kanngiesser^{167a, b} found aerial shoots 9, 14, 19 and 44 years old.

In connection with his observations concerning the Jenen's chalk roses, Kanngiesser makes some remarks respecting the famous so-

called thousand-year old rose in the cathedral cemetery of Hildesheim,^{168a, b} which stands in a very protected location and enjoys the best of care as a local attraction. According to Kanngiesser, this thousand-year old rose, a specimen of *Rosa canina* forma *luteiana* Lam., might be at least 400 years of age. This great age does not apply, however, to the visible stem, which probably can scarcely exceed 50 years, but rather to the root system. The badly weathered root-stock had a circumference of 92 cm. in 1883 when it was inspected.

Rosa dumetorum Thuill. The oldest shoot of this species was 14 years of age.

Rosa rubiginosa L. Kanngiesser¹⁶⁹ found a 13-year old shoot.

Rosa rubrifolia Vill. There was a 13-year old specimen in Hildesheim.

Rosa repens Scop. and **R. capreolata Neill.** These species often attain a height of over 200 feet on the old walls of churches and castles in England and Scotland. This is a significant size and a correspondingly significant age.¹⁷⁰

Sorbus Aria Crantz. May become 50 to 200 years old.

Sorbus domestica L. A trunk 43 cm. thick which was exhibited at the Nuremberg exposition showed 140 annual rings. Stützer makes mention of a trunk more than one meter thick which stands in Vrindsberg and which is estimated to be at least 200 years old.

Sorbus torminalis Crantz. Becomes more than 230 years old.

Sorbus Aucuparia L. Seldom over 80 years old.

Pirus communis L. Up to 300 years old.

Pirus Malus L. An apple tree in Marbach is among the largest yet described. At breast height it is 3.63 m. in circumference; its height is 18 m. and its age calculated to be 200 years.

Crataegus oxyacantha L. Kanngiesser¹⁷¹ gives a detailed report of the oldest English hawthorn which stands in the garden of the Resource Company of Soest in Westphalia. In the third decade of the 16th century it was already regarded as an old tree and now is certainly over 400 years of age.

Cotoneaster integerrima Med. A crippled bush only 15 cm. tall was 13 years old.

Prunus avium L. Seldom becomes more than 100 years

old. Kanngiesser mentions a cherry tree whose age was supposed to be between 300 and 400 years.¹⁷¹

***Prunus Padus* L.** Sixty-year old specimens are known.

***Prunus spinosa* L.** Becomes 47 years old. A very much-branched bush had an age of 28 years and two others were, respectively, 23 and 28 years old. The oldest investigated were 40 and 47.¹⁷²

***Dryas octopetala* L.** Kraus¹⁷³ counted 25 annual rings in one specimen 4 mm. thick, and in another at the Russia-Lapland limit of vegetation Kihlmann¹⁷⁴ found 108 rings.

PAPILIONACEAE

***Robinia pseudoacacia* L.** Can become more than 200 years old.

***Cytisus Laburnum* L.** Specimens 30 years old are known.

***Cytisus Adami* L.** In the Jardin des Plantes in Paris there is a specimen which in March, 1906, had a basal circumference of 40 cm. and was more than 60 years old.¹⁷⁵

***Spartium scoparium* L.** Can become 14 years old.

***Wistaria sinensis* Sweet.** Was introduced into Europe in 1816. There are specimens 50 and 60 years old.

THYMELAEACEAE

***Daphne Mezereum* L.** The Count of Leiningen¹⁷⁶ collected a stem 2½ cm. thick which showed 38 rings.

***Daphne Laureola* L.** Kanngiesser¹⁷⁷ reports a 26-year old root-stock upon which was an 11-year old stem.

ELAEAGNACEAE

***Hippophaë rhamnoides* L.** On the beach at Howachs a specimen 60 cm. in circumference was found whereupon we may conclude that the sea-buckthorn can attain considerable age.

***Elaeagnus angustifolia* L.** A specimen in Hildesheim had the unusual height of 12 m., a diameter of 35 cm. and an age of 33 years.

MYRTACEAE

***Myrtus communis* L.** In Raddington there stood a specimen of the Spanish broad-leaved variety which in 1724 was 6 m. tall and 156 years old.¹⁷⁸

***Eucalyptus*.** The genus *Eucalyptus* with its numerous

species is among the characteristic representatives of the Australian flora. The most important is *E. amygdalina*. According to measurements, this species attains the unbelievable height of 155 m. and a basal circumference of 30 m.^{170a, b} Its dimensions thus surpass those of the redwoods and it is, accordingly, the tallest tree on earth. The trunk remains unbranched for a considerable distance, its relatively sparse branching beginning only at a height of 70 to 90 m. where the circumference is still 12 m.

By actual measurement, according to F. von Müller, one specimen of *E. amygdalina* was 394 feet tall, when its dimensions in English feet is expressed in the Parisian unit. The tallest tree of this species from the sources of the Yarra and the Latrobe was estimated at 470 feet. The tallest tree in West Australia, the Kaori, *E. collosca*, is said to have measured 375 feet. A specimen of *E. amygdalina* 143.5 m. tall was found at the foot of Mount Bau Bau.

Eucalyptus trees grow very rapidly, as may be observed from the frequently planted *E. globulus* in Europe, for example, along the Riviera. At the Villa Thuret near Antibes certain of these trees attained a height of 10 m. within 4 years.¹⁸⁰ In 20 years these trees usually become more than 20 m. tall.

Unfortunately, I have been unable to find any information concerning the maximum age of *E. amygdalina*, not even in Joly's¹⁸¹ account. If we bear in mind, however, that the eucalyptus is a very rapidly growing tree its age can hardly exceed that of the sequoias, and if so not by much.

CORNACEAE

Cornus sanguinea L. Becomes 50 years old and, according to some, even 80.

Cornus Mas L. One tree is described whose root-stock was 2½ m. in circumference and whose age was estimated at 300 years.¹⁸²

ARALIACEAE

Hedera Helix L. There are numerous examples of very old English ivy. Only two will be mentioned here which I take from Kanngiesser's account.

There is a very old ivy at the mountain castle of Seebenstein in lower Austria, the mother plant of which is supposed to be about 200 years of age. In Gignac near Montpellier there was an ivy 1.8 m. in circumference with an estimated age of about 440 years.

ERICACEAE

Rhododendron. Exotic species in England have already attained ages between 40 and 45 years.

Rhododendron ferrugineum L. The oldest specimen with ten stout stems was 40 years of age.¹⁸³

Rhododendron hirsutum L. One individual 1.7 cm. in diameter from the Achensee was 54 years old.

Phyllodoce coerulea Bab. A specimen from the Kola peninsula was rotten in the center but still showed 35 annual rings.

Loiseleuria procumbens Desv. A specimen from the same peninsula was 64 years old.

Arctostaphylos alpina Spreng. More than 84 years old.

Arctostaphylos Uva ursi Spreng. A specimen from Russian Lapland was 80 years old. A very well developed specimen collected by Count Leiningen was 1.4 cm. in diameter.

Calluna vulgaris Salisb. The greatest observed age is 42 years.

Erica Tetralix L. The oldest specimen from the Dutch heather country was 10 years of age.

Erica carnea L. Count Leiningen collected a specimen only 5½ mm. thick but 21 years old.

Vaccinium uliginosum L. Kraus¹⁸⁴ examined stems from Kaiser-Franz-Josephs-Land which were 85 to 93 years old. On the Bavarian moor Count Leiningen found a specimen 1½ cm. thick and 25 years old.

Vaccinium Myrtillus L. In the mountains this plant becomes larger and its longevity greater than in the valley. The greatest age observed was 25 years¹⁸⁴ and in another case 28 years.

GENTIANACEAE

Gentiana. Osterwalder¹⁸⁵ says that the age of the root-stock of *Gentiana lutea* can not be exactly determined because in the case of old specimens it is never certain whether the entire rhizome is still present. In young root-stocks, however, 15 to 25 annual rings can be counted and in the case of two plants whose entire rhizomes were still intact, ages of 28 and 40 years were definitely found. This author remarks also that many other specimens permit the conclusion that ages of 50 to 60 years may be attained. In discussing excess growth beyond a vegetative maximum and con-

sequent death of the plant, he continues with the following remarks. "With the fifth to eighth annual flowering period, based upon successive flowering periods of the same part of the rhizome, even the apparently uninjured plant exceeds its vegetative maximum. Like younger injured ones, these old root-stocks are often able to produce flowering shoots for a long time but the latter gradually decline in size, vigor and blossoming, until finally they produce only one or two flowering whorls. Diameter growth of the root and root-stock diminishes and soon is no longer anatomically discernible; the leafy growing point stands upon a base which becomes smaller and smaller from year to year. With almost uniform growth in length the youngest parts of the rhizome become thinner until the growing points die. This decadence may be prolonged for 20 years or more, during which time the lower portions of the rhizome together with their roots may decay and completely disappear."

PRIMULACEAE

Cyclamen. In Moeller's "Deutsche Gärtnerzeitung" I find the statement that the bulb of *Cyclamen europaeum* can become 60 years old.

OLEACEAE

Olea europaea L. Whoever has observed olive trees in southern Europe soon arrives at the conclusion that these trees can become very old. Religious legends and historical tales bespeak this also. In the shade of the eight specimens on the Mount of Olives in Jerusalem the Nazarene is said to have roamed. According to Pausanius, the olives on the Acropolis and at Delos are numbered among the oldest trees of Greece.

Picconis says the largest olive tree stands near Pescia. Its circumference is 21 feet and De Candolle the elder calculated its age at 400 years.¹²⁶

Ligustrum vulgare L. A stem $4\frac{1}{2}$ cm. thick on the Würzburger Wellenkalk was 23 years old.¹²⁷

Fraxinus excelsior L. Attains considerable size. Very old trees are estimated to be 200 to 250 years of age.

CAPRIFOLIACEAE

Lonicera coerulea L. Small stems from the Kola peninsula were 7 to 14 mm. thick and 9 to 16 years old.

Lonicera Periclymenum L. Can attain an age of 38 years.

Viburnum Lantana L. A small stem 21 years old has been reported.

Viburnum Opulus L. A shoot $2\frac{1}{2}$ m. tall arising from a root-stock was 11 years old.

Sambucus nigra L. A very large elder near Tölz has a circumference of 2.3 m. at a height of one meter and may be about 100 years old, according to Kanngiesser.

Sambucus racemosa L. Can become 20 years old.

Bignonia Catalpa L. In the park of Wachenheim a large specimen was 55 to 60 years old, according to Kanngiesser.

LABIATAE

Teucrium montanum L. Kanngiesser saw specimens 30, 31 and 33 years old. The above-ground parts are short-lived, the subterranean relatively long-lived.

Thymus chamaedrys Fries. In this plant, too, the above-ground portions are of very short duration. A stem with 14 annual rings has been observed.

GLOBULARIACEAE

Globularia cordifolia L. Though this little shrub remains small and adheres closely to the ground, it can attain an age of between 10 and 35 years.

SUMMARY

The following table has been compiled in order to present a brief summary of the maximum ages observed among the phanerogams already discussed. The succession in the table is such that, independent of their relationship, those are first listed which are distinguished by the greatest longevity, followed by those of shorter life and finally by the short-lived. It must again be noted that the ages are only approximate because the longevity of any species varies within certain limits and the figures given are often based only on estimates.

Many annuals, biennials and other plants of ephemeral life might be included among the last mentioned and short-lived forms, but they are generally well known and therefore need not be noted.

It is common knowledge that there are plants which bear fruit only once during their lives, and others which do so several times or frequently. The former, upon De Candolle's suggestion, are known as monocarpic and the latter as polycarpic. Those which

REVIEW OF THE MAXIMUM PERIODS OF LONGEVITY OF VARIOUS PHANEROGAMS

| Name | Maximum age | Circumference in meters | Diameter | Height in meters |
|---------------------------------------|---------------|-------------------------|----------|------------------|
| <i>Adansonia digitata</i> | 5150 | | | 10 |
| <i>Sequoia</i> (Big-tree) | 4000-5000 | | 10 m. | 142 |
| <i>Ficus religiosa</i> | 2000-3000 (?) | | | |
| <i>Cupressus sempervirens</i> | 2000-3000 | | 3 m. | 50 |
| <i>Taxus baccata</i> | 900-3000 | | | |
| <i>Juniperus communis</i> | 2000 | 2.75 | | |
| <i>Taxodium distichum</i> | 2000 | | | |
| <i>Cedrus Libani</i> | 1200-1300 | | | |
| <i>Platanus</i> sp. | 1300 (?) | | | |
| <i>Picea excelsa</i> | 200-1200 | | | |
| <i>Pinus cembra</i> | 1200 | 7.65 | | |
| <i>Tilia</i> sp. | 800-1000 | 16.5 | 4.50 m. | |
| <i>Quercus</i> sp. | 500-1000 | | | |
| <i>Fagus sylvatica</i> | 600-930 | | | |
| <i>Abies alba</i> | 300-800 | | | |
| <i>Dammara australis</i> | 700-800 | | | |
| <i>Castanea vulgaris</i> | 500-700 | 9 | | |
| <i>Tilia platyphyllos</i> | 700 | 14.5 | | |
| <i>Olea europaea</i> | 700 | 6.4 | | |
| <i>Pinus nigra</i> | 600 | | | |
| <i>Populus alba</i> | 300-600 | 12 | | |
| <i>Ulmus</i> sp. | 300-600 | 16.68 | | 36 |
| <i>Pinus sylvestris</i> | 500 | | | |
| <i>Acer platanoides</i> | 400-500 | 5.10 | | 25 |
| <i>Pinus strobus</i> | 400-450 | | | |
| <i>Pinus canariensis</i> | 440 | | | |
| <i>Juglans regia</i> | 300-400 | | | |
| <i>Ulmus effusa</i> | 300-400 | 6.43 | | 20 |
| <i>Rosa canina</i> (Root-stock) | 400 | | | |
| <i>Crataegus oxyacantha</i> | 400 | | | |
| <i>Prunus azium</i> | 100-400 | | | |
| <i>Pinus glutinosa</i> | 100-300 | | | |
| <i>Populus nigra</i> | 300 | 8 | | |
| <i>Pinus communis</i> | 300 | | | |
| <i>Cornus mas</i> (Root-stock) | 300 | 2.5 | | |
| <i>Carpinus betulus</i> | 250 | | | |
| <i>Fraxinus excelsior</i> | 250 | | | |
| <i>Sorbus torminalis</i> | 230 | | | |
| <i>Dracaena Draco</i> | 185-200 | 17.45 | 4.82 m. | 22 |
| <i>Acer campestre</i> | 150-200 | 3.4 | | |
| <i>Acer montanum</i> | 200 | | | |
| <i>Sorbus aria</i> | 50-200 | | | |
| <i>Sorbus domestica</i> | 140-200 | | 43 cm. | |
| <i>Pinus malus</i> | 200 | 3.63 | | 18 |
| <i>Robinia pseudoacacia</i> | 200 | | | |
| <i>Hedera helix</i> | 200 | | | |
| <i>Myrtus communis</i> | 156 | | | 6 |
| <i>Corylus avellana</i> | 150 | 2.20 | | 10 |
| <i>Salix alba</i> | 150 | 7 | | |
| <i>Populus tremula</i> | 150 | 3.73 | | 21 |

REVIEW OF THE MAXIMUM PERIODS OF LONGEVITY OF VARIOUS PHANEROGAMS
 (Continued)

| Name | Maximum age | Circumference in meters | Diameter | Height in meters |
|--|-------------|-------------------------|----------|------------------|
| <i>Buxus sempervirens</i> . . . | 150 | | | |
| <i>Salix fragilis</i> | 140 | | | |
| <i>Salix arctica</i> | 130 | | 6.2 mm. | |
| <i>Betula odorata</i> | 124 | | | |
| <i>Betula verrucosa</i> | 120 | | | |
| <i>Dryas octopetala</i> | 25- 108 | | | |
| <i>Welwitschia mirabilis</i> | 70- 100 | | | |
| <i>Carpinus duinenensis</i> | 100 | | | |
| <i>Ostrya vulgaris</i> | 100 | | | |
| <i>Corylus colurna</i> | 100 | | | |
| <i>Magnolia acuminata</i> | 100 | | | |
| <i>Rhamnus cathartica</i> | 100 | | | |
| <i>Vitis vinifera</i> | 80- 100 | | | |
| <i>Sambucus nigra</i> | 100 | 2.30 | | |
| <i>Fockea capensis</i> | 100 | | | |
| <i>Salix myrsinites</i> | 99 | | 65 mm. | |
| <i>Vaccinium uliginosum</i> | 93 | | | |
| <i>Arctostaphylos alpina</i> | 84 | | | |
| <i>Sorbus aucuparia</i> | 80 | | | |
| <i>Cornus sanguinea</i> | 50- 80 | | | |
| <i>Arctostaphylos Uraursi</i> | 80 | | | |
| <i>Betula nana</i> | 80 | | 12 mm. | |
| <i>Loiseleuria procumbens</i> | 64 | | | |
| <i>Cyclamen europaeum</i> | | | | |
| (Tuber) | 60 | | | |
| <i>Cytisus Adami</i> | 60 | | | |
| <i>Histaria sinensis</i> | 60 | | | |
| <i>Bignonia catalpa</i> | 60 | | | |
| <i>Rhododendron hirsutum</i> | 54 | | | |
| <i>Prunus spinosa</i> | 47 | | | |
| <i>Calluna vulgaris</i> | 42 | | | |
| <i>Clematis vitalba</i> (Root-stock) | 41 | | | |
| <i>Rhododendron ferrugineum</i> | 40 | | | |
| <i>Daphne mezereum</i> | 38 | | | |
| <i>Lonicera periclymenum</i> | 38 | | | |
| <i>Globularia cordifolia</i> | 38 | | | |
| <i>Phyllodoce coerulea</i> | 35 | | | |
| <i>Teucrium montanum</i> | 33 | | | |
| <i>Elaeagnus angustifolia</i> | 33 | | | |
| <i>Rhamnus frangula</i> | 30 | | | |
| <i>Cytisus laburnum</i> | 30 | | | |
| <i>Vaccinium myrtillus</i> | 28 | | | |
| <i>Helianthemum canum</i> | 28 | | | |
| <i>Daphne laureola</i> | 26 | | | |
| <i>Berberis vulgaris</i> | 24 | | | |
| <i>Helianthemum chamaecistus</i> | 24 | | | |
| <i>Ligustrum vulgare</i> | 23 | | 4.5 cm. | |
| <i>Erica carnea</i> | 21 | | 5.5 mm. | |
| <i>Viburnum lantana</i> | 21 | | | |
| <i>Sambucus racemosa</i> | 20 | | | |

REVIEW OF THE MAXIMUM PERIODS OF LONGEVITY OF VARIOUS PHANEROGAMS
(Continued)

| Name | Maximum age | Circumference in meters | Diameter | Height in meters |
|--|-------------|-------------------------|----------|------------------|
| <i>Helianthemum polifolium</i> | 17 | | | |
| <i>Polygonatum multiflorum</i> (Root-stock) .. | 15 | | | |
| <i>Thymus chamaedrys</i> .. | 14 | | | |
| <i>Spartium junceum</i> .. | 14 | | | |
| <i>Rosa dumetorum</i> .. | 14 | | | |
| <i>Rosa rubrifolia</i> .. | 13 | | | |
| <i>Cotoneaster integririma</i> | 13 | | | |
| <i>Erica Tetrallix</i> | 10 | | | |

fruit only once may be one-, two-, several- or many-year plants, according as sporogenesis or fructification requires one, two or more years. After ripening of the fruit they die.

The expressions, annual and biennial, unfortunately do not carry a clear meaning and appear to be inappropriately chosen, mathematically considered as well as otherwise.

Those monocarpic species which during a single year produce fruit several times and then die after each such production, are usually¹⁻⁸ designated as being ephemeral; those which fruit only once annually and then die, as annual; and finally, those which live during two successive vegetative periods, as biennial. Those whose lives terminate with fructification only after several years are designated as perennials.

Except for the last of these categories, these terms are not always employed in the senses indicated. Kirchner^{1,9a, b} applies the term annual, for instance, to those monocarpic plants which germinate in autumn and flower and fruit the following spring; when they germinate in the spring and fruit the following spring he calls them biennial. Also the term ephemeral appears to me to be unfortunately chosen because, according to its etymology, it easily gives the impression that ephemeral plants live for only a few days. This is true, to be sure, of many cryptogams, such as molds, but not of phanerogams, for there are no flowering plants whose lives terminate in only a few days; truly ephemeral plants require at least several weeks, e.g., *Senecio vulgaris*, *Stellaria media*.

Aside from the fact that these terms are not consistently employed

in the same sense, it is not always certain in the case of many plants whether they are annual, biennial or of longer duration. This is especially true of those inhabiting subtropical and tropical regions and many are erroneously designated as annuals which they certainly are not. *Ricinus*, for example, germinates, flowers, fruits and then is destroyed by frost at the end of the vegetative period in our part of the world; it is often falsely regarded, consequently, as annual. Actually, however, it is a polycarpic plant of several years' duration which becomes even tree-like in warm climates. The same is true also of *Maurandia*, *Lophospermum*, *Calophora* and certain species of *Capsicum*.^{1900, b}

I am obliged to my colleague, Richard Wettstein, for the following interesting case of the prolongation of life as a result of climatic change. He says that in September, 1901 (at the close of the dry season before the beginning of the vegetative season which corresponds to our spring), he visited a German settler in San Bernardo in southern Brazil, who was cultivating in his garden all kinds of little European plants as a reminder of his Fatherland. Among them were *Linum usitatissimum* whose seeds he had secured from his old home. These plants were partly in fruit, partly in flower, almost one meter tall, very twiggy and possessed in particular a very woody stem three to four centimeters thick at the ground from which numerous branches arose.

Upon his asking, he was informed by the owner of the garden that the latter had seeded out these plants during the early months of 1900, that they had flowered and fruited continually for one year and that he previously had other plants which were still older. The plants that he saw, one specimen of which he brought along in alcohol, were at that time almost two years old and had grown during three successive vegetative periods, one rainy and two dry seasons.

With us, he says, the strictly annual *Linum usitatissimum* sometimes becomes perennial without interference of flower and fruit formation and has undoubtedly evolved from a perennial species. However, the plant which he saw in Brazil had not resumed the ability to form annual rings but had developed a distorted woody structure by continual growth.

The preparation given me by Wettstein was a cross-section from a stem of elliptic contour whose maximum diameter was 24 mm.

CHAPTER III
LONGEVITY AND RELATED PHENOMENA
**VARIOUS PERIODS OF LONGEVITY AND THEIR
PROBABLE CAUSES**

It is apparent, on the basis of general experience as well as that of the preceding examples, culled from the entire plant kingdom, that individual periods of longevity may be very different from one another though characteristically constant within a species. They vary from a few hours to thousands of years and may exceed by far that of the longest-lived animal. Though the elephant can become about 200 years old and the whale even several centuries in age, nevertheless, these animals can not compete with the sequoias and dragon trees of thousands of years when it comes to matters of longevity. The greatest periods are found, therefore, among plants and of them there are some living today which were contemporaries of events that occurred before the birth of Christ.

The questions now arise: What is the reason for one period being so short, another long or even exceedingly great? Are there one or more causes and does this variation have some purpose?

Since the shortest-lived plants are to be found among the smallest and the longest-lived among the largest, it appears that size is not without some significance in matters of longevity. If we contemplate how much organic matter must be manufactured and how many million cell divisions must take place before so complicated a structure as a tree is fully developed, we can readily understand that a greater span of time must be allotted the tree than an alga, a yeast cell, a moss, or the common whitlow-grass. Shrubs, too, generally live for much shorter periods than the larger trees. However, size alone can not control longevity, for size and longevity do not always run parallel. The annual sunflower, *Helianthus annuus*, attains the stately height of two meters or more, and, in addition, completes its entire life within one period of vegetative growth, while *Dryas octopetala*, a very small species adhering to the ground, can live for several years, even for decades. Numerous other lowly shrubs, such as *Asalea procumbens*, *Empetrum nigrum* and *Arctostaphylos Uva ursi*, grow to be many years old, while a great number of herbaceous annuals, such as maize and certain species of

Chenopodium and *Amaranthus*, become much larger but live for only a few months. Nevertheless, size must influence longevity to a certain extent in a great many cases. Other factors, however, also play a more or less important rôle.

Weismann examined the question as to whether or not longevity of animals is correlated with the intensity of their metabolism, and he arrived at wholly negative conclusions.¹⁹¹ The bird, for example, though it possesses an unusually high rate, attains considerable age.

Weismann was not concerned about a possible influence which the rate of metabolism may have upon the longevity of plants, but if we give thought to the matter it appears as though the rate does have a definite relation, in many cases, with long-livedness. Intensity of respiration can indeed be regarded, to a certain degree, as a measure of intensity of metabolism, since we know, for example, that flowers exhibit an unusually high rate of respiration, leaves less so and stems still less, and that the longevity of these organs parallels these rates, *i.e.*, flowers live only a short period, leaves for a longer period and stems still longer. Furthermore, if we compare succulents, characterized by slow growth and reduced respiration, with tender herbaceous plants of active respiration, it is likewise apparent that the succulents, to the extent that their respiration is low, are generally rather long-lived, while the others are short-lived. This is brought out by the following table¹⁹² in which are indicated the quantities of oxygen in cubic millimeters absorbed by certain plants per hour and per gram of fresh weight at 12° to 15° C.:

| | | | |
|--------------------------------------|-------|--------------------------------|--------|
| <i>Cercus macrogonus</i> | 3.00 | <i>Lupinus albus</i> | 44.10 |
| <i>Opuntia cylindrica</i> | 6.80 | <i>Tulipa europaea</i> | 89.60 |
| <i>Opuntia maxima</i> | 15.30 | <i>Faba vulgaris</i> | 96.60 |
| <i>Phyllocactus grandiflorus</i> ... | 28.70 | <i>Mirabilis jalappa</i> | 120.00 |
| | | <i>Triticum sativum</i> | 291.00 |

It will be observed that the cacti, which live for decades, exhibit a low rate of respiration, while non-succulent forms, which live scarcely one year, possess a much more intensive rate.

Furthermore, organs whereby plants perpetuate their kind, such as tubers, bulbs, root-stocks and seeds, are likewise characterized when fully developed by a relatively low rate of respiration.

All this indicates that the rates of assimilatory and dissimilatory processes can have a part in longevity, because by a rapid rate of

metabolism in those plants which produce fruit only once, the foods and reserve materials necessary for fructification and seed production are produced in sufficient quantity more rapidly, and earlier reproduction and death are thereby made possible. It must not be claimed, however, that other factors are not involved.

According to Weismann, it is not the purpose of Nature to assure to an animal at maturity the greatest possible length of life but rather the shortest longevity consistent with a normal reproductive period. He adds expressly that this tendency pertains only to animals and not to plants.¹⁹³ It appears to me, however, that it applies also to those plants which bear fruit only once. These germinate, develop and, as soon they are fully grown, they store reserve materials and then proceed to fructification and seed production. These developments involve such a great drain upon the entire plant that it dies and Nature sacrifices the individual unmercifully as soon as perpetuation of the species has been provided for.

This principle of the greatest possible abbreviation of a natural life does not apply to polycarpic plants, however, for we know that many such forms, particularly trees and shrubs, continue to live a long while, sometimes for many centuries, after attaining maturity. Serious consideration will show that this latter situation, too, must be regarded as a purposeful provision, for we dare not forget that woody plants which produce fruit frequently, many times require decades for their maturity before they become sexually of age. Büsgen¹⁹⁴ has shown, for instance, that the flowering age of beech trees growing in the open is between 40 and 50 years, whereas in a closed stand it is between 60 and 80 years. In the open, oaks flower after 40 years; otherwise, not until they are 80 to 100 years of age. Other examples of this nature are as follows:

| | | |
|-----------------------------------|---------------------|------------------------------|
| <i>Castanea vesca</i> | 40 to 60 years | (Stump sprouts, 6 years) |
| Hazel | 10 " | (Cuttings, 3 years) |
| Hornbeam | 20 to 30 " | (Stump sprouts, 10 years) |
| Elder | 12 to 20 " | (Under cover, 40 years) |
| Birch | 10 to 12 " | (" " 30 ") |
| Elm | About 40 " | |
| Linden | About 25 " | |
| <i>Acer campestre</i> | 25 " | |
| <i>Acer pseudo-platanus</i> | 30 to 40 " | |
| <i>Acer platanoides</i> | A few years earlier | |
| Ash | 30 to 40 " | |
| Spruce | 30 to 50 " | (Under cover 60 to 70 years) |

| | | | |
|-------------------|----------|---|---|
| Fir | 60 to 70 | " | |
| Larch | 20 | " | (Flowers at 10 years but seeds do not germinate) |
| Scotch pine | 15 | " | (Under cover 30 to 40 years) |

In view of the fact that a tree has to assimilate food for decades in order to attain a certain size and to acquire a certain amount of reserve materials, it would not be in the interest of the species if Nature were to sacrifice the tree after it had produced fruit and seed the first time. The very first descendants would then have to begin all over again, as it were, and assimilate food for decades once more in order, in their turn, to arrive at the first subsequent production of seeds. This round-about way is to be avoided and it appears more practical, therefore, for the mature tree to be used as much as possible as a source of seed in order to produce a large progeny and thus provide for the preservation of the species in a more effective and more economical manner. This objective is best achieved by a prolongation of life, thereby making possible frequent production of seed (polycarpy) during the course of decades, sometimes of centuries. An abundant production of seed during a long period of time appears all the more desirable because seeds frequently do not have a chance to germinate, either because they fall upon unsuitable places or because they are eaten by animals or destroyed in some other manner. Moreover, many plants perish in the struggle for existence before producing their first seeds and it must be regarded as expedient for the tree to live long after first maturing seeds and then to continue producing them.

If we now examine what is known concerning the longevity of plants we arrive at certain general conclusions which may be summarized in the following three statements, designating as youth the period from germination to the first production of seed, and the subsequent period, characterized by production of progeny and finally ending in death, as the bearing time:

1. Plants with brief youth have short longevity.
2. Plants with a long youthful period generally enjoy great longevity.
3. A long youthful period is usually followed by a long and often very extended bearing time.

The last two statements can be made only as general principles, for it happens, though relatively seldom, that many monocarpic plants die after a fairly long youthful period, directly subsequent to the



FIG. 13. A century plant, *Agave americana*, Tonto National Forest, Arizona. Photo by U. S. Forest Service.

first production of fruit and seed. *Fourcroya*¹⁹⁵ offers a striking example of this and among the palms are some, as certain species of *Corypha*, which live for many years and whose entire life is devoted to the storing of reserve material and to the ultimate conversion of their single growing point into a huge inflorescence and mass of fruit. As soon as this happens, the palm dies. *Agave americana*, in its native climate in Mexico, has a youth of eight to ten years and then develops its huge inflorescence, produces fruit and perishes. If we prolong its youth by altering the conditions under which it grows, as is easily done and as will be considered at greater length in a later chapter, the development of flowers is postponed and ultimate death as well. This indicates very markedly how dependent the longevity of monocarpic plants is upon the length of the youthful period.

In the foregoing, attention has been directed toward some of the factors which influence longevity, but there undoubtedly are others. Just as the general development of a plant is controlled by the soil, climate and general surroundings, so is its longevity similarly subject to change. By adaptation to new conditions an annual may be converted into a biennial or into a plant of several years' duration, and *vice versa*. In view of this, we can understand why, for example, the number of annual plants changes at a certain elevation. Investigations of Bonnier and Flahault¹⁹⁶ upon the flora of the Dauphiné reveal the following percentages of annuals in the indicated regions:

| | |
|--|-----|
| Below the conifers at 200 to 600 m. elevation | 60% |
| In the region of conifers and meadows, 600 to 1800 m. | 33% |
| In the upper alpine regions above 1800 m. | 6% |

It is apparent from these figures that with increasing altitude the number of annual species declines significantly, evidently because with increasing altitude the period of vegetative growth becomes so short, the climate so rigorous and the living conditions so unfavorable for annuals, that many of them do not find sufficient favorable time within one year to complete their life cycle from germination to fruit production.

In agreement with these relationships the same authors find that annuals diminish in number the farther they extend toward northern latitudes. In Paris at 49° N., 45% of the plants are annuals;

only 30% at Oslo at 59.55° N.; and at Listad, 61.40° N., only 26% are annuals.

Arenaria serpyllifolia and *Poa annua* are annuals in the lowland and of longer life in the mountains; and annuals of the lowlands may be represented in the high mountains by species having longer life, viz.: in the Alps, *Draba verna* is represented by *D. lacvigata*, and *Viola tricolor* by *V. lutea*.

According to Kanngiesser, the longevity of woody plants increases at their limits of distribution because of relatively unfavorable influences of climate and soil.

The following table is taken from Hildebrand's¹⁹⁷ work and is based upon the flora of Freiburg i. Br., excepting the lower Alps. The figures indicate the numbers and percentages of species in the four classes and show to what degree certain sites influence these plants of different periods of longevity. Moisture relations are particularly significant.

PERCENTAGES OF ANNUALS, BIENNIALS AND PERENNIALS ON DIFFERENT SITES

| | Annuals | Biennials | Perennials | |
|--|-----------|-----------|------------|--------------|
| | | | Herbs | Trees/Shrubs |
| Stony and sandy dry places | 44 21.3% | 22 10.7% | 134 65% | 6 3% |
| Dry meadows | 7 5.7% | 5 4.0% | 111 90.3% | |
| Wet meadows with ditches or swamps . | 34 11.7% | 6 2.1% | 227 77% | 27 9.2% |
| Woods and thickets . | 5 2.5% | 3 1.5% | 130 65% | 61 31% |
| Water | 1 2.6% | | 37 97.4% | |
| Banks, roads and borders of fields | 23 | 12 | 8 | |
| Fields and similar cultivated areas ... | 121 88.8% | | 15 11.2% | |

The figures indicate that in water, with its more constant conditions, perennial polycarpic plants predominate, while annuals remain almost wholly in the background with only 2.6%. A similar situation obtains with respect to the vegetation of woods and thickets. We note, furthermore, though it is not especially significant, that annuals already appear in dry meadows, to a larger extent in wet meadows, and especially along highways, banks and fields where they predominate.

We can certainly conclude from these facts that location definitely bears some relation to longevity. Though a particular site embraces a complexity of chemical and physical factors, it must be emphasized that, in addition to these factors of location, others, too, of an internal and as yet not understood nature, can influence longevity.

LONGEVITY AND SYSTEMATIC RELATIONSHIP

We have not made any reference, so far, to the question as to whether longevity may in some way be associated with phylogenetic position, whether related species, genera or even families and higher groups reveal their relations by identical or at least similar periods of longevity. Hildebrand¹⁹⁸ was concerned with this question in his notable work and much that follows in the present discussion is founded upon that contribution.

INDIVIDUALS OF THE SPECIES

Individuals of one and the same species possess approximately equal periods of longevity, though, it must be admitted, of no constant magnitude but rather fluctuating about a definite average, sometimes more, sometimes less. Those which are not inclined to vary in longevity withstand new conditions with greater difficulty than do those possessing the tendency.

Among annuals which are to a certain degree fixed in the matter of longevity are *Erigeron canadensis*, *Polygonum aviculare* and *Papaver Rhoeas*. Among those which are rather variable under the influence of cultivation and other conditions, might be mentioned: *Brassica Napus*, *B. Rapa*, *Spinacia oleracea*, *Secale cereale* and cultivated species of wheat and barley. There are also species to be regarded as biennials in one country but as annuals in a warmer land, e.g., *Melilotus officinalis*, *Trifolium incarnatum*, *Oenothera biennis*, *Isatis tinctoria*, and others.

SPECIES OF A GENUS

To a much greater extent than among individuals, we can observe that amid species there are some with rather stable and others with variable periods of longevity. Many genera are known:

1. whose species are annuals almost without exception: *Nigella*, *Specularia*, *Helianthus*, *Melampyrum*, *Galeopsis*, *Amaranthus*, etc.
2. whose species exhibit perennial growth by means of subter-

anean organs for the most part: *Thalictrum*, *Anemone*, *Caltha*, *Symphytum*, *Pulmonaria*, etc.

3. whose species are mostly shrubby: *Berberis*, *Rosa*, *Rhamnus*.
4. whose species are only trees: *Tilia*, *Fraxinus*, *Juglans*, *Ulmus*, *Quercus*, *Fagus*, *Pinus*.

In contrast to these genera there are those whose members are more or less different with respect to longevity. Within a genus there may be both annuals and biennials (*Tordylium*), annuals and perennials (*Adonis*, *Biscutella*, *Stellaria*, *Geranium*, *Lamium*, *Asperula*), annuals in addition to shrubs (*Sideritis*, *Chenopodium*, *Salsola*), biennials and perennial herbs (*Heracleum*, *Cirsium*, *Aconitum*), or perennial herbs and woody plants (*Clematis*, *Sambucus*, *Aristolochia*, *Rubus*). Further details may be found in Hildebrand's account.¹⁹⁹

GENERA OF A FAMILY AND THE HIGHER GROUPS

If differences in longevity are shown by species and genera it is not surprising that this is true to an even greater degree among families and higher groups. As Hildebrand has shown, there is such a close relation between the longevity of a species and that of its genus, that if members of a species vary, then the species of its genus do so likewise, and, conversely, in a genus whose species do not vary in longevity, individuals of the species are constant. The same relation is shown by genera of a family.

Though within a family periods of longevity may be very different, there are families, however,

1. whose genera are composed exclusively of herbaceous perennials: Nymphaeaceae, Orchidaceae, Hydrocharitaceae, Colchicaceae.
2. whose members are exclusively woody, i.e., trees or shrubs: Magnoliaceae, Anonaceae, Aceraceae, Celastraceae, Rhamnaceae, Amygdalaceae, Pomaceae, Oleaceae, Cupuliferae, Salicaceae, Coniferae.

In contrast with these, the great majority of families consist of members characterized by very diverse periods of longevity and vegetative habits: Leguminosae, Compositae, Labiatae, Urticaceae. It is not surprising, therefore, to find an even greater difference between the orders and still larger divisions of the plant kingdom. Among them, too, there is a degree of similarity, for plants lowest in the scale of evolution and phylogenetically among the oldest, the thallophytes, are featured, for the most part, by delicate structure

and short life, while among higher cryptogams there is a development of woody stems or perennial rhizomes and of long life. In the case of gymnosperms, woody stems and great longevity attain the ultimate dominance. And among monocotyledons long life prevails in the palms and shrubby forms, while short-lived annuals are relatively rare.

So we see that the relationships of plants can be reflected in their periods of longevity, though not necessarily, and this should not be surprising in view of the physiological feature that internal factors are often tied up with the type of development and as the former change so do the related forms.

UNLIKE PERIODS OF LONGEVITY OF THE TWO SEXES

Does the male plant live as long as the female? We have long been inclined to assume that among annuals the male perishes first because as soon as it has developed pollen and effected fertilization of the female flower, its purpose is fulfilled and further vegetative growth is unnecessary. The female plant, on the other hand, must provide for further development of the fruit, and to this end it needs its organs of assimilation, the leaves. For this reason it must prolong its life until the fruit is fully matured.

In the case of many animals²⁰⁰ this is the course of events. The males of the Strepsiptera, remarkable little parasites of bees, live only two to three hours in a mature state while the wingless and worm-like female dies only after eight days. The life of the female in this case is 64 times that of the male. Also in the vine louse, *Phylloxera vastatrix*, the males live for a much shorter period than do the females and we find similar relations among the rotifers and in many copepods, Cirripedia, bees and ants. Other examples in the animal kingdom are given by Korschelt.²⁰¹

It is surprising that this relationship, so far as it pertains to plants, has not heretofore been investigated. I have been unable to find any pertinent information upon the subject but have carefully studied the matter myself in the case of hemp, *Cannabis sativa*. About 100 hemp seeds were sown in a garden on June 2, 1918, and cared for. The seedlings grew well and flowered in July and August. Toward the middle of August, however, the male plants began to turn yellow, while the female were still dark green.

The former died between the first and fifteenth of September, drying out from the bottom upward, and became strawy, while the female plants were almost all still green. Only at the end of September or beginning of October did they, too, decline under ripening of the seed. On this basis I can say that the pistillate plants of hemp live two to four weeks longer than the staminate.

It is very obvious also from field culture that the staminate plants of hemp die sooner than the pistillate. After the staminate flowers have cast their pollen, the leaves and stems become yellow and strawy, the pistillate plants remaining deep green and alive for some time. On August 20 I once observed in the fields of Villach in Kärnten that the male plants had already died to a large extent while the pistillate were still luxuriant. We can likewise observe in bisexual flowers of many plants that the male organ, *i.e.*, the androecium, dies before the stigma and style belonging to the gynoecium. Examples of this are furnished by the bell-flower, *Campanula*, and by crane's bill, *Geranium*.

I do not want to fail to mention that the sterile flowers of *Hydrangea aspera* live longer than the fertile ones. The perianth segments of the sterile blossoms become green on the morphologically upper side and red on the lower which later is directed upward.

Ginkgo, as another example, is a dioecious tree and no means has yet been devised to distinguish between trees of the two sexes until they produce sex organs.²⁰² I have gained the impression in Europe and in Japan,²⁰³ however, that the two sexes are distinguished by producing and dropping their leaves at different times. The staminate trees usually open their buds about a week earlier than the pistillate and shed their leaves correspondingly earlier in autumn. In the botanical garden of Vienna there is a large staminate tree upon which a pistillate scion was grafted years ago, and the latter has given rise in the course of time to a large branch abundantly bearing fruit. With considerable precision one can readily observe on this tree every autumn this difference in time with respect to leaf production and leaf fall. When the staminate tree has shed its leaves the pistillate branch still bears its foliage.

Heinricher²⁰⁴ tells about another ginkgo three meters tall in the botanical garden of Innsbruck whose terminal shoot he removed and replaced by the grafting of a staminate shoot secured from

Würzburg. It is not stated whether the stock was pistillate, but in agreement with my own observations Heinricher found that the staminate scion always sprouted earlier than the stock; contrary to expectation, however, it remained longer in foliage. As is so often true in grafting, it is possible in this case that at the point of union the descending stream of assimilates was obstructed by an irregular development of tissues, as might happen in girdling, and that the scion, consequently, was unusually well nourished²⁰⁵ and retained its leaves longer in a green and living condition.

Particular interest attaches to the fact established by Correns that in the biennial dioecious *Trinia glauca* the numerical ratio of the two sexes of plants shortly before flowering is 1:1 and that the mortality of the two is the same at that time, but that, beginning at the initiation of flowering, almost all the staminate plants rot off at the crown of the roots, usually long before flowering ceases, while only a few of the pistillate plants die. The ratio of staminate plants which die to the pistillate ones that perish is 19:1 and this relation is rather constant during the entire blossoming period. According to Correns,²⁰⁶ the disease which destroys the staminate plants in such a devastating manner is caused by an infection resulting in decay of the root and drying-out of the main flowering shoot as well as of the lateral shoots. The agent of this infection is still unknown. If, now, the staminate plants are more subject to infection and perish sooner than the pistillate, there must be a constitutional difference between the sexes, probably of a chemical nature. This has already been shown in the case of many animals and it is my opinion that investigations directed especially upon this point will disclose chemical differences between the two sexes of still other organisms. The distinctions which are revealed in the structure of dioecious flowers may well go hand in hand with corresponding chemical differences.

Weber²⁰⁷ has called attention to a striking susceptibility of staminate plants toward frost injury. Male plants of the dioecious *Datisca cannabina* freeze every autumn upon the first slightest frost, while the pistillate, which at this time begin to ripen their fruit, last for several weeks longer. He mentions especially that the male plants do not naturally perish earlier but succumb because of greater susceptibility to the frost.

In the case of certain mosses, e.g., dioecious species of *Polyt-*

richum, the leaves of the female plants enjoy a shorter longevity than do those of the antheridial plants. Those of the archegonial plants die after formation of sporogonia, living for only one year, while those of the antheridial plants remain alive for two years.

As de Vries showed not long ago,²⁰⁸ premature death may set in if some characteristic necessary to life is not inherited and is thus omitted from the plant. Though this situation does not concern dioecious plants and, strictly speaking, is beyond consideration here, it may, however, be mentioned. Many plants produce seedlings whose cotyledons remain white or yellow without becoming green. They produce either no chlorophyll or only such a very small amount that they are unable to produce additional leaves, and, therefore, they soon die. This can be seen with respect to certain plants in fields and also in gardens where great masses of seeds are sown. The following table from de Vries states the percentages of yellow and white seedlings found among certain species:

| | | | |
|--------------------------------|----------|---------------------------------|-----------|
| <i>Antirrhinum majus</i> | up to 6% | <i>Scrophularia nodosa</i> ... | up to 15% |
| <i>Clarkia pulchella</i> | " " 13% | <i>Trifolium incarnatum</i> .. | " " 6% |
| <i>Papaver Rhoeas</i> | " " 30% | <i>Chrysanthemum segetum</i> .. | " " 13% |
| <i>Papaver rufifragum</i> ... | " " 30% | <i>Linaria vulgaris</i> | " " 25% |
| <i>Polygonum Fagopyrum</i> " " | 12% | <i>Trifolium pratense</i> | " " 13% |

The percentages decline in other cases as low as 1 to 2 %.

De Vries was finally led to the conclusion that certain qualities essential for development can be lost in the same way as other mutations and that races then arise of whose seedlings one quarter and at times even one half die prematurely.

So much for annuals and for plants of longer duration. It is not known how the two sexes of dioecious perennials behave as far as longevity is concerned; whether pistillate oaks, willows, poplars and the ginkgo live longer or only just as long as the staminate trees, and further investigations along this line would be very commendable.

THE LONGEVITY OF ORGANS

FLOWERS

The flower of an angiosperm is a metamorphosed shoot adapted for definite functions and consisting usually of very different organs. The latter can display a variety of longevities insofar as one dies before the other. In the Papaveraceae, for instance, the calyx is very temporary, soon falling, and shortly thereafter the

corolla and stamens follow suit. Among the Primulaceae, on the other hand, the corolla and stamens are shed rather early, while the calyx may be retained for months in a living condition. It is not easy, therefore, to say just how long the flower persists, for its component parts behave differently in this respect. When in the following discussion reference is made to the longevity of flowers, it must be understood, therefore, that the period of longevity extends from the first opening of the blossom to the final withering or shedding of its important parts (calyx, stamens).

So conceived, the duration of flowers among various plants lasts from three hours to three months. The shortest-lived constitute the so-called ephemeral flowers and in the following table von Kerner²⁰⁰ has gathered together the hours of opening and closing of a number of one-day flowers:

PERIODS OF LONGEVITY OF ONE-DAY FLOWERS

| Plant | Opens | Closes |
|-------------------------------------|-----------|-------------|
| <i>Allionia violacea</i> | 3-4 A. M. | 11-12 A. M. |
| <i>Roemeria violacea</i> | 4-5 " " | 10-11 " " |
| <i>Cistus creticus</i> | 5-6 " " | 5-6 P. M. |
| <i>Tradescantia virginica</i> | 5-6 " " | 4-5 " " |
| <i>Iris arenaria</i> | 6-7 " " | 3-4 " " |
| <i>Hemerocallis fulva</i> | 6-7 " " | 8-9 " " |
| <i>Convolvulus tricolor</i> | 7-8 " " | 5-6 " " |
| <i>Oxalis stricta</i> | 8-9 " " | 3-4 " " |
| <i>Hibiscus Trionum</i> | 8-9 " " | 11-12 Noon |
| <i>Erodium Cicutarium</i> | 8-9 " " | 4-5 P. M. |
| <i>Portulaca grandiflora</i> | 8-9 " " | 6-7 " " |
| <i>Calandrinia compressa</i> | 9-10 " " | 1-2 " " |
| <i>Drosera longifolia</i> | 9-10 " " | 2-3 " " |
| <i>Arenaria rubra</i> | 10-11 " " | 3-4 " " |
| <i>Portulaca oleracea</i> | 10-11 " " | 3-4 " " |
| <i>Spergula arcensis</i> | 10-11 " " | 3-4 " " |
| <i>Sisyrinchium anceps</i> | 11-12 " " | 4-5 " " |
| <i>Mirabilis longiflora</i> | 7-8 P. M. | 2-3 A. M. |
| <i>Cereus grandiflorus</i> | 8-9 " " | 2-3 " " |
| <i>Cereus nycticalus</i> | 9-10 " " | 2-3 " " |

If we arrange these short-lived blossoms according to the time they are open, we secure the following:

PERIODS OF LONGEVITY OF ONE-DAY FLOWERS

| Plant | Hours open |
|--------------------------------------|------------|
| <i>Hibiscus Trionum</i> | 3 |
| <i>Calandrinia compressa</i> | 4 |
| <i>Portulaca oleracea</i> | 5 |
| <i>Drosera longifolia</i> | 5 |
| <i>Arenaria rubra</i> | 5 |
| <i>Spergula arvensis</i> | 5 |
| <i>Cereus nycticalus</i> | 5 |
| <i>Sisyrinchium anceps</i> | 5 |
| <i>Roemeria violacea</i> | 6 |
| <i>Oxalis stricta</i> | 7 |
| <i>Mirabilis longiflora</i> | 7 |
| <i>Cereus grandiflorus</i> | 7 |
| <i>Allionia violacea</i> | 8 |
| <i>Erodium Cicutarium</i> | 8 |
| <i>Iris arenaria</i> | 9 |
| <i>Convolvulus tricolor</i> | 10 |
| <i>Tro. escautia virginica</i> | 10 |
| <i>Portulaca grandiflora</i> | 10 |
| <i>Cistus creticus</i> | 12 |
| <i>Hemerocallis fulva</i> | 14 |

As indicated in the table, short-lived flowers open either between early morning and noon, at approaching twilight, or at night. Among them are those which open between five and seven o'clock in the evening, remaining so during the entire night and the following forenoon, and which do not close until noon or evening of the next day, generally 24 hours after first opening. They include several species of thorn-apple and evening primrose, *Datura Metel*, *D. Stramonium*, *Oenothera biennis*, *Oe. grandiflora*, *Morina Persica*, *Mirabilis Jalappa* and *Echinocactus Tetani*. The flowers of these plants open and close only once but there are others which do so several times and whose longevity, accordingly, is longer. In this category may be mentioned *Glaucium corniculatum*, *G. luteum*, *Papaver alpinum*, *Linum tenuifolium*, *Rubus idacus*, *Potentilla erecta* and *Opuntia nana*.

The following table based upon von Kerner's data and my own, indicates the longevity of flowers which live from two to many days. From these figures we observe that the time within which the

PERIODS OF LONGEVITY OF VARIOUS FLOWERS

| Plant | Floral Longevity in Days | Plant | Floral Longevity in Days |
|---|--------------------------------|--|--------------------------------|
| <i>Centunculus minimus</i> | 2 | <i>Digitalis purpurea</i> | 6 |
| <i>Dianthus prolifer</i> | 2 | <i>Erythraea pulchella</i> | 6 |
| <i>Epilobium collinum</i> | 2 | <i>Heimerocallis flava</i> | 6 |
| <i>Geranium pratense</i> | 2 | <i>Lilium album</i> | 6 |
| <i>Papaver somniferum</i> | 2 | <i>Oxalis lasiandra</i> | 6 |
| <i>Potentilla atrosan-</i> | | | |
| <i>guinea</i> | 2 | <i>Ranunculus acris</i> | 7 |
| <i>Rosa arvensis</i> | 2 | <i>Pelargonium zonale</i> | 7 |
| <i>Saponaria Vaccaria</i> | 2 | <i>Eranthis hiemalis</i> | 8 |
| <i>Sinapis arvensis</i> | 2 | <i>Hepatica triloba</i> | 8 |
| <i>Veronica aphylla</i> | 2 | <i>Parnassia palustris</i> | 8 |
| <i>Lonicera Caprifolium</i> | 3 | <i>Saxifraga bryoides</i> | 8 |
| <i>Potentilla formosa</i> | 3 | <i>Cyclamen europaeum</i> | 10 |
| <i>Agrimonia Eupa-</i> | | | |
| <i>torium</i> | 3 | <i>Crocus sativus</i> | 12 |
| <i>Aphyllanthes monspe-</i> | | | |
| <i>liensis</i> | 3 | <i>Saxifraga Burseriana</i> | 12 |
| <i>Galium infestum</i> | 3 | <i>Vaccinium oxycoccus</i> | 18 |
| <i>Helianthemum alpestre</i> | 3 | <i>Cattleya labiata</i> | 30 |
| <i>Lychnis diurna</i> | 4 | <i>Vanda coerulea</i> | 30 |
| <i>Sagina saxatilis</i> | 4 | <i>Cypripedium insigne</i> | 40 |
| <i>Sedum atratum</i> | 4 | <i>Odontoglossum</i> sp. | 40 |
| <i>Scilla Liliohyacinthus</i> | 4 | <i>Dendrobium crassinode</i> | 42 |
| <i>Telephium Imperati</i> | 4 | <i>Epidendrum Lind-</i> | |
| | | <i>leyanum</i> | 50 |
| <i>Sanguinaria canadensis</i> | 4 | <i>Phalaenopsis grandiflora</i> | 50 |
| <i>Escholtzia californica</i> | 5 | <i>Oncidium cruentum</i> | 60 |
| <i>Fritillaria Meleagris</i> | 5 | <i>Cypripedium villosum</i> | 70 |
| <i>Scilla sibirica</i> | 5 | <i>Odontoglossum Rossii</i> | 80 |
| <i>Erythraea Centaurium</i> | 5 | <i>Phalaenopsis Schilleriana</i> | 90-135* |
| <i>Linum viscosum</i> | 5 | | |

* In the Gardeners Chronicle of May 17, 1873, I find the statement that blossoms of *Phalaenopsis Schilleriana* have lasted from Christmas to May 7, a period of 4½ months. After coming into flower, the plant stood in a conservatory at 10° to 13° C., a relatively low temperature, which accounted for the long life of the flowers.

flowers of various plants remain living is, relatively speaking, not great, but that it varies, as has already been noted, between three and 2160 hours. Von Kerner says with justification: "This strik-

ing difference is related to the amount of pollen in the individual flowers as well as to the number of flowers per stalk and depends also upon whether or not the stigmas of the flowers concerned are exclusively insect-pollinated. Flowers provided with many stamens and abundant pollen, as those of poppy, citrus and portulaca, always possess short longevity, while, conversely, those with only one anther, as most orchids, remain fresh for weeks. If the plant puts forth only one flower annually, as is true of *Galanthus*, *Pirola uniflora*, *Paris quadrifolia* and the different species of *Trillium*, or when the flowers are only two or three in number, as in *Cypripedium calceolus* and tropical orchids of the genera *Oncidium*, *Stanhopea* and *Cattleya*, these single flowers long remain fresh and open.

It may so happen, in spite of all the means of allurements at the disposal of a flower, that it remains unvisited by insects for weeks at a time because of unfavorable weather conditions. If the blossom is so constructed that in the absence of pollen-bearing insects there is no development of viable seed, then plants producing only one or a few such short-lived blossoms would develop no seeds at all during a year's time. It is very advantageous, therefore, if flowers of this nature persist as long as possible; the longer they remain fresh and open the greater is the likelihood that insects laden with pollen from other flowers will visit them at least once.

The same effect is achieved if many short-lived flowers are borne on a plant during the course of a year, especially if the blossoms do not open at the same time but successively and if, in addition to cross-pollination, self-pollination is possible. The chances for fertilization and seed production are then just as great. An especially good example of this is seen in the perennial *Tradescantia virginica* where during a period of two months the plant uninterruptedly produces blossoms which last for only a day, new ones opening each day and closing in the afternoon.

LEAVES

As compared with flowers, leaves are of greater duration; compared with the entire plant, however, they are rather short-lived, sometimes conspicuously so, except in those cases where their death is approximately simultaneous with that of the entire plant. Unfortunately there is not much information concerning their age^{210a-c} and it is particularly unfortunate that Hansgirg's²¹¹ work, though devoted to foliar biology, makes no mention of foliar longevity.

The little that I do find in the literature may be summarized as follows, together with some of my own observations.

Under the most favorable circumstances the leaves of annuals attain the age of the plants which bear them, usually that of only one vegetative period, namely, several months. This is true of the lower as well as of more advanced species. Moss leaves, for instance, live at the most only one vegetative period and then die as they turn brown.

Pteridophytes. Among ferns (Filicineae), too, there are numerous species whose leaves fulfill their function within one vegetative period. The fronds of *Pteris aquilina*, for example, are green during the summer only, while those of tree ferns remain so for years. Horsetails often retain their green aerial organs for only one period of vegetative growth and then die together with the sheath-like leaves. In *Equisetum hiemale* I find the leaves already dead at the beginning of the second season though the stem is still alive. The leaves of *Marsilea quadrifolia*, of most species of *Selaginella* in our greenhouses, of *Ophioglossum vulgatum*, and of native species of *Botrychium* live only one year or during one period of vegetative development.

Gymnosperms. With respect to gymnosperms, the table on pages 99 and 100 may be consulted. According to observations of von Zederbauer,²¹³ a change in the longevity of needle leaves goes hand in hand with changes in climatic conditions, for spruces in the mountains retain their leaves longer than do those on the plains. The table on page 97 illustrates how the average longevity of certain coniferous leaves increases with elevation above sea level.

Zederbauer's idea appears plausible when he says that extension of the life of needle-leaves is an adaptation to a climate otherwise curtailing the life of the tree, and that it is a very economical arrangement for employing light in assimilation to the greatest extent.

In view of the foregoing remarks, it might be expected that conifers secured from different climates would differ in the longevity of their leaves, a situation which is suggested by the fact that other characteristics adapting a tree to a particular habitat are inherently retained. According to Zederbauer, this is actually the case. He was enabled to make the following observations upon spruces from a variety of climates and which Cieslar²¹⁴ cultivated in the woods

LONGEVITY OF CONIFER LEAVES

| Elevation in meters | Longevity of needles in years | | | |
|---------------------------------------|-------------------------------|----------------------------|----------------------------|--------------------------|
| | <i>Picea excelsa</i> | <i>Pinus silestris</i> | <i>Pinus austriaca</i> | <i>Pinus montana</i> |
| 230 (Mariabrunn) | 4-6 | 2-3 | 2-4 | 4-5 |
| 600 (Puchberg am Schneeberg) | 7-8 | 4-5 | 4-6 | |
| 1400 (Schneeberg, N.E.) | 9 | | | 7 |
| 1750 (Schneeberg, N.E.) | 10-13 Bushy | | | 8-11 |

about Vienna. The average longevity of the spruce needles from the indicated places and stipulated elevations were:

| | | |
|-----------------------------|--------|---------|
| Finland | | 8 years |
| Attergau in Austria | 1380m. | 8-9 " |
| Achenal in the Tyrol | 900m. | 6 " |
| " " " " | 1300m. | 6 " |
| " " " " | 1600m. | 6 " |
| Edling near Wolfsberg | 460m. | 5 " |

Though we note in these figures certain variations attributable to climate, locality and other factors, nevertheless, the longevity of the leaves is characteristically constant within certain limits for each species.

Monocotyledons.—Monocotyledons produce leaves which vary greatly with respect to longevity. In numerous bulbous forms, such as *Hyacinthus*, *Tulipa*, *Narcissus*, *Fritillaria*, *Galanthus*, *Leucojum*, *Gagea*, *Scilla* and *Ornithogalum*, leaves appear in the spring, flowers and fruit soon follow, and before the seeds develop the leaves lie on the ground, already yellowed or completely dried out. The maximum age of such foliage is often only one to a few months, and in the case of *Amaryllis lucida*, according to Grisebach,²¹² only ten days are needed for development of leaves and flowers and for ripening of the fruit.

The other extreme we find among many palms whose leaves often persist for years. If we bear in mind that the palm leaf can attain extraordinary size, for which a great amount of food mate-

rial is needed, it is quite understandable that the longevity of such organs should be prolonged and that the plant should not rid itself of them so soon. *Dracaena*, *Yucca*, *Aloë*, *Agave*, *Pandanus* and other monocotyledonous genera often possess leaves which they retain for two to three years, probably even longer. Since exact figures are lacking, a systematic investigation of foliar longevity among monocotyledons would be worthwhile. We are in a better position concerning the next group.

Dicotyledons.—In a small contribution upon the age of evergreen leaves in about half a dozen plants, Hoffmann marked newly emerging leaves of greenhouse plants in the botanic garden of Gies-sen by fastening with thread small sheets of tinfoil about their petioles. He thereby noted the time up to yellowing or shedding of the leaves.

On the occasion of a visit to Italy, Kraus disclosed the foliar age in numerous other evergreen plants by that of the twigs bearing the leaves. It is well known that among many conifers, as well as with deciduous trees, the age of twigs can be judged from outward appearances; each increment of growth corresponding to one vegetative period is located above the one immediately preceding it and is distinguished from it by successive changes in the thickness of the stem, by color differences, by markings of bud-scale scars, or by the crowding of leaves at the beginning of each year. If such indications are lacking, the age can be determined, in the case of dicotyledons, also by counting the annual rings. In monocotyledons, to be sure, this means is not available, for annual rings are not present.

Particular attention must yet be directed to one point which, so far as I know, has not heretofore been considered. When we speak of the duration of leaves it is tacitly understood, as in the following discussion, that the leaf begins its period of longevity with the opening of the bud and concludes it at the time of leaf fall. This conception is not entirely correct, however, for the actual beginning of any prospective leaf is concealed within the bud close to the growing point where it develops bud scales and remains enclosed by them, among our woody plants, until the following spring, finally to develop further at that time. As a concrete example, the elder develops its foliage buds shortly after sprouting and the tiny leaves which constitute the buds long remain immature and thus pass the

winter, attaining full development only the next year. A leaf of the elder lives, then, not one but two vegetative periods. This accounts for the fact that leaves falling spontaneously in autumn, yellowed or not, as a rule do not fall in a dead condition but die on the ground, usually through drying out. In order, then, to estimate foliar longevity correctly, these two circumstances must be taken into consideration, as well as the fact that in determining foliar longevity we are dealing not with a fixed value but with one varying between certain limits. The leaves of one tree, even those of the same twig, may show different periods of longevity, even when they apparently are subjected to the same external conditions. It can also be readily observed that short and horizontal or inclined branches of laurel retain their leaves for one or two years while the long, rod-forming and vertical shoots retain theirs for four to five years.

It may be noted also that leaves of sucker shoots usually become older, those of younger plants generally live longer than those of older ones, and needles of the Scots pine last longer when exposed to light than in the shade. In the last case nutrition appears to me to play a significant rôle to the extent that better nutrition results in longer life. This seems all the more likely because, as will be shown later by experiments, the longevity of cotyledons can be conspicuously prolonged by abundant feeding.

Summary.—The following table presents a review of the approximate periods of foliar longevity among various gymnosperms and dicotyledons:*

REVIEW OF THE PERIODS OF LONGEVITY OF VARIOUS SPECIFIC
KINDS OF LEAVES

| Species | Foliar longevity in years | Remarks |
|-----------------------------------|------------------------------|---------|
| Conifers | | |
| <i>Cupressus funebris</i> | 1-2 | |
| " <i>horizontalis</i> | 1-2 | |
| <i>Libocedrus decurrens</i> | 1-2 | |

* See the original German edition, p. 79, for the authorities.

REVIEW OF THE PERIODS OF LONGEVITY OF VARIOUS SPECIFIC
 KINDS OF LEAVES—(Continued)

| Species | Foliar longevity in years | Remarks |
|---------------------------------|------------------------------|---------|
| <i>Pinus pinea</i> * | 2 | |
| “ <i>maritima</i> | 2 | |
| “ <i>canariensis</i> | 2 | |
| “ <i>silvestris</i> | 2 & more | |
| “ “ | 2-8 | |
| “ <i>laricio</i> | 2 & more | |
| “ “ | 3-6 | |
| “ <i>Pinsapo</i> | 11-15 | |
| “ <i>excelsa</i> | 1-2 | |
| “ <i>Cembra</i> | 3-6 | |
| “ <i>montana</i> | 5-13 | |
| <i>Taxodium</i> sp. | 2-3 | |
| <i>Sequoia</i> sp. | 2-4 | |
| <i>Juniperus oxycedrus</i> | 3-4 | |
| <i>Cephalotaxus Fortunei</i> | 3-5 | |
| <i>Sciadopitys verticillata</i> | 2-8 | |
| <i>Podocarpus Koraiana</i> | 4-7 | |
| <i>Taxus baccata</i> | 6-8 | |
| “ “ | 8-10 | |
| <i>Cunninghamia sinensis</i> | 8 | |
| <i>Abies excelsa</i> | 3-5 | |
| “ “ | 4-14 | |
| “ <i>pectinata</i> | 5-10 | |
| “ “ | 5-11 | |
| “ <i>holophylla</i> | 2-5 | |
| “ <i>Nordmanniana</i> | 3-5 | |
| <i>Cedrus libani</i> | 1-4 | |
| <i>Araucaria brasiliensis</i> | 15 | |
| “ <i>Bidevilli</i> | 15 | |
| Gnetaceae | | |
| <i>Welwitschia mirabilis</i> | to 100 | |
| <i>Ephedra tatarica</i> | 1 | |
| “ <i>procera</i> | 1 | |
| “ <i>Gerardiana</i> | 1 | |
| “ <i>campulopoda</i> | 1 | |
| “ <i>helvetica</i> | 1 | |

* May²¹⁵ gives the following periods of foliar longevity: Spruces (*Picea nigra*, *P. rubra*, *P. alba*, *P. obovata*, *P. orientalis*, *P. sitchensis*) 6 to 7 years; Firs (*Abies Nordmanniana*, *A. cephalonica*, *A. Pinsapo*, *A. balsamea*, *A. grandis*, *A. sibirica*) 7 to 8 years; Pines (*Pinus rigida*, *P. Taeda*, *P. ponderosa*, *P. Jeffreyi*, *P. Strobus*, *P. excelsa*) 3 years; Douglas-fir (*Pseudotsuga Douglasii*) 4 to 6 years.

REVIEW OF THE PERIODS OF LONGEVITY OF VARIOUS SPECIFIC
 KINDS OF LEAVES—(Continued)

| Species | Foliar longevity in years | Remarks |
|--------------------------------------|------------------------------|---|
| Dicotyledons | | |
| <i>Schinus Molle</i> | 1 | |
| <i>Senecio Petasites</i> | 1 | |
| <i>Ficus stipulata</i> | 1 | |
| <i>Salvia officinalis</i> | 1 | |
| <i>Arbutus Andrachne</i> | 1 | |
| <i>Quercus lanata</i> | 1 | |
| <i>Veronica salicifolia</i> | 1-2 | |
| <i>Myrsine africana</i> | 1-2 | |
| <i>Nerium Oleander</i> | 1-3 | |
| <i>Evonymus japonicus</i> | 1-2 | |
| <i>Eriobotrya</i> | 1-3 | |
| <i>Photinia</i> | 1-4 | |
| <i>Ilex Perado</i> | 1-2 | Leaves usually one year old, seldom two years or older. |
| <i>Phillyrea angustifolia</i> | 1-2 | |
| <i>Persca gratissima</i> | 1-2 | |
| <i>Magnolia grandiflora</i> | 1-2 | |
| <i>Ceratonia</i> | 1-2 | |
| <i>Eucalyptus Globulus</i> | 1-2 | |
| <i>Olea europea</i> | 2 | |
| <i>Prunus Laurocerasus</i> | 1-3 | |
| " <i>lusitanica</i> | 1-3 | |
| <i>Arbutus Unedo</i> | 1-2 | |
| <i>Ligustrum japonicum</i> | 1-3 | |
| <i>Cocculus laurifolius</i> | 2 | |
| <i>Mahonia Aquifolium</i> | 1-3 | One- and two-year-old leaves equally common. |
| " <i>Fortunei</i> | 1-3 | |
| <i>Pittosporum undulatum</i> | 1-2 | |
| <i>Rhamnus Alaternus</i> | 1-2 | |
| <i>Grevillea robusta</i> | 1-2 | |
| <i>Camphora</i> | 1-2 | |
| <i>Erica arborea</i> | 1-5 | |
| <i>Laurus nobilis</i> | 4 | |
| <i>Quercus Ilex</i> | 1-4 | |
| " <i>Suber</i> | 1-3 | |
| <i>Rosmarinus officinalis</i> | 2-3 | |
| <i>Melaleuca hypericifolia</i> | 2-3 | |
| <i>Pittosporum Tobira</i> | 3-5 | Leaves regularly two years old, often three to four. |
| <i>Pistacia Lentiscus</i> | 3-5 | |
| <i>Ilex Aquifolium</i> | 2-4 | |
| " " | 2 | |
| <i>Hackea acicularis</i> | 3-5 | |

REVIEW OF THE PERIODS OF LONGEVITY OF VARIOUS SPECIFIC
 KINDS OF LEAVES—(Continued)

| Species | Foliar longevity in years | Remarks |
|---------------------------------------|------------------------------|---------|
| <i>Vaccinium vitis idaea</i> | 1-2.4 | |
| <i>Rhododendron ponticum</i> | 1-2 | |
| <i>Hedera Helix</i> | 1-2.3 | |
| <i>Prunus laurocerasus</i> | 1.5 | |
| <i>Eugenia caparridifolia</i> | 2-5 | |
| “ <i>australis</i> | 1-2 | |
| <i>Camellia japonica</i> | 2 | |
| <i>Pittosporum undulatum</i> | 2-4 | |
| <i>Pseudopanax crassifolium</i> | 3-4 | |
| <i>Callistemon violaceum</i> | 3-5 | |

Finally, some observations upon the maximum age of evergreen leaves which I was in a position to make during my stay of several years in Japan:²¹⁶

| | |
|---------------------------------------|-----|
| <i>Ligustrum japonicum</i> | 2 |
| <i>Ilex crenata</i> | 2 |
| <i>Quercus</i> sp. | 2 |
| <i>Aucuba japonica</i> | 2-3 |
| <i>Thea Sasangua</i> | 2 |
| <i>Erionymus japonicus</i> | 1-2 |
| <i>Thea japonica</i> | 2 |
| <i>Viburnum odoratissimum</i> | 2 |
| <i>Lomaria japonica</i> | 2 |
| <i>Ilex latifolia</i> | 3 |
| <i>Cryptomeria japonica</i> | 4 |
| <i>Pinus densiflora</i> | 2 |
| <i>Pasania</i> sp. | 4 |
| <i>Illicium anisatum</i> | 2-4 |
| <i>Torreya nucifera</i> | 5 |
| <i>Litsea japonica</i> | 5-7 |
| <i>Osmonthus Aquifolium</i> | 5 |
| <i>Sciadopitys verticillata</i> | 8 |
| <i>Abies firma</i> | 15 |

Examination of all these figures shows the following:

The leaves of *Welwitschia mirabilis*²¹⁷ possess the greatest longevity, attaining a maximum age of 100 years. Next are the needles of conifers and among them the longest periods are shown by the flat individually developed leaves of various Taxineae and Abietineae and of the genera *Araucaria* and *Cunninghamia*. Among the Cu-

pressineae, the junipers occupy an intermediate position, as do the sequoias and certain two-leaved species of pine among the Abietineae. Their period of foliar longevity is two to three or four to five years. Relatively short-lived among conifer leaves are those of *Cupressus* and *Libocedrus*.

The broad leaves of dicotyledons are shorter-lived. *Hackea*, *Laurus*, *Quercus*, *Ilex*, *Pistacia*, *Callistemon* and *Pittosporum* possess foliar longevity up to five years and there are others, though not many, which show three to four years. The majority of dicotyledons, however, are in the one-year class, not infrequently showing a tendency to retain their leaves for two years.

We must not fail to mention that many species of broad-leaved trees are conspicuously distinguished from one another by their time of foliation. This can readily be observed in a mixed wood when the foliage appears in spring. Even in the same species, as the beech, or, as I have often observed, in chestnut and linden, one can see that individuals under exactly the same conditions do not sprout at the same time, but some earlier, others later, and that they maintain this rhythm each year. Since the progeny of such plants behave the same as their parents with respect to early or late foliation, a heritable feature must be involved.²¹⁸

In general, it may be said, aside from exceptions, that the life of leaves is relatively shorter than that of shrubs and trees as a whole. I shall soon touch upon this point and attempt to find a plausible explanation.

Though the relatively short longevity of most leaves is generally well known, we have not heretofore been concerned with the causes involved. Why do leaves fall when they have attained a certain age? Or why do they die usually after the first period of vegetative growth, even though they may not be discarded by means of an abscission layer? Is their death controlled merely by external factors or is it inherent?

Continued increase of ash content as a contributing factor in the death of leaves. Water taken up by the roots of a tree ascends the trunk together with dissolved mineral salts and then continues into the leaves of the crown. The leaves transpire, giving off the water in the form of vapor, while the mineral salts remain in the leaves. The same is true of herbaceous plants. Since this tran-

spiration always takes place when the atmosphere is not saturated with moisture and since during the course of one vegetative period immense amounts of water are given off by the leaves, quantities greater than from all other parts of the plant, there must result a gradual accumulation of mineral salts in the leaves. In other words and on the assumption that incombustible materials are not removed from the leaves in such quantities as they enter them, the leaves must continually become richer in ash content and finally become the most ash-laden of all the organs of the plant. This idea is fully confirmed by ash analyses and in the following table we note the much greater percentage of ash content in the dried material of fully developed leaves as compared with that of their green and less transpiring stems.²¹⁹

ASH ANALYSES OF CERTAIN SPECIFIC KINDS OF LEAVES AND STEMS

| | Leaves | Stems |
|----------------------------------|--------|-------|
| <i>Lupinus luteus</i> | 6.06 | 3.86 |
| <i>Brassica Rapa</i> | 20.84 | 9.18 |
| <i>Humulus Lupulus</i> | 13.60 | 3.74 |
| <i>Primula farinosa</i> | 11.73 | 5.90 |
| <i>Nicotiana Tabacum</i> | 11.87 | 7.73 |
| <i>Anethum graveolens</i> | 15.03 | 9.86 |
| <i>Gossypium herbaceum</i> | 7.86 | 1.81 |

The ash content of fully developed leaves varies in many cases between 8 and 12%, based on the dried material. Frequently much greater values can be found:²¹⁹

| | |
|---------------------------------|--------------|
| <i>Solanum tuberosum</i> | 18.19-25.77% |
| <i>Myosotis arvensis</i> | 17.85 |
| <i>Scleranthus annuus</i> | 17.20 |
| <i>Urtica dioica</i> | 17.82 |
| <i>Ricinus communis</i> | 20.11 |
| <i>Beta vulgaris</i> | 29.23 |
| <i>Ranunculus repens</i> | 18.00 |
| <i>Senecio jacobaea</i> | 23.24 |
| <i>Nicotiana Labacum</i> | 22.97 |
| <i>Xanthium spinosum</i> | 17.97 |

From these tables we see that the large percentages of ash content belong to plants having leaves which, for the most part, are relatively soft and herbaceous and which transpire abundantly.

If there is a relation between intensity of transpiration and ash content to the extent that greater transpiration results in greater ash content, then those leaves which are provided with some protective adaptation against excessive transpiration, as the evergreen needles of conifers, must have a comparatively low ash content. This is actually the case, as the following table shows:

| | |
|-------------------------------|-------------------------|
| <i>Larix decidua</i> | up to 2.48% |
| <i>Pinus silvestris</i> | " " 1.48 |
| <i>Pinus austriaca</i> | " " 1.80 ²²⁰ |

It is also indicated here that the softer and greater transpiring leaves of the larch, which live for only one season, contain more ash than do the lesser transpiring needles of the pine, which retain its leaves for several years.

The fact that the foliar ash content of woody plants often increases continually with age is also of importance for my further considerations. Rissmüller²²¹ found the following percentages of ash in the leaves of *Fagus sylvatica*:

ASH ANALYSES OF BEECH LEAVES

| | May 26 | June 26 | July 26 | Aug. 25 | Sept. 26 | Oct. 26 | Nov. 7 |
|----------------------|--------|---------|---------|---------|----------|---------|--------|
| Dried material | 23.35 | 40.21 | 43.64 | 50.74 | 47.42 | 40.37 | 45.55 |
| Fresh material | 4.67 | 5.20 | 7.45 | 9.03 | 8.90 | 10.80 | 11.42 |

Dulk²²² found the following percentages for leaves of a 20-year-old beech, which had not yet borne fruit:

ASH ANALYSES OF BEECH LEAVES

| | May 26 | June | July | Aug. | Sept. | Oct. | Nov. |
|----------------------|--------|-------|-------|-------|-------|-------|-------|
| Dried material | 20.76 | 34.32 | 36.00 | 37.66 | 36.32 | 37.15 | 33.63 |
| Pure ash | 4.68 | 3.95 | 4.78 | 5.52 | 5.58 | 5.91 | 6.39 |

Concerning a concomitant increase in the ash content of aging leaves, Ebermayer says:²²³ "The total mineral content increases with

progressive age; the young leaves in spring are always poorer in mineral materials than the discarded leaves of autumn. According to Rissmüller, the ash content in leaves of a red beech in the botanical garden of München increased from 4.67% of the dry weight in spring (May) to 11.42% in fall (Nov.). In the leaves of an approximately 25-year-old beech it increased from 3.95% to 6.93% and in those of a red beech from 5.50% to 9.91%. The leaves of a black locust contained 6.25% pure ash in May and 11.74% in October, and in the leaves of a birch the ash content rose from 3.84% in May to 4.68% in October. Dried young leaves from a specimen of *Pinus austriaca* contained 1.63% in June and 2.25% in October; one-year-old needles of the same tree showed 1.81% in May, 2.30% in October; two-year-old needles showed 2.72% in May and 2.59%

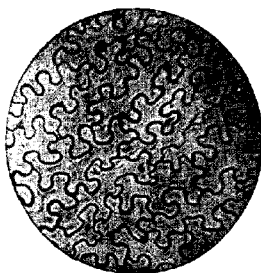


FIG. 14. Silicified skeleton of the foliar epidermis of *Pteris aquilina*. $\times 180$. Original.

in October; and three-year-old needles showed 3.12% in May, 3.28% in October."

Though the absolute ash content generally increases with age, it must not be thought that ash substances can not at times be removed from the leaves. On the basis of recent investigations by Swart,²²⁴ we know, for instance, that there is a decrease in the amount of phosphorus and potassium in yellowing aging leaves because the plant withdraws their compounds from the leaves during the process of yellowing and before the fall of the leaves, compounds which occur in Nature usually only in very small amounts. In this manner such valuable materials are conserved. If in spite of this translocation the ash content still increases with age, the increase is attributable principally to accumulating quantities of

calcium and silicic acid which remain in the leaves. Calcium oxalate, once precipitated within the plant, remains, aside from certain exceptions, as waste material where it is deposited; calcium carbonate likewise remains where it is formed, incrusting cystoliths, hairs or other membranes,²²⁵ and the calcium which so frequently is disguised within the cell membranes, closely associated with the wall material, may in all probability behave in a similar fashion.

In judging the higher ash contents it must be remembered that mineral materials are not equally distributed in the individual tissues and cells but that certain regions are favored. In leaves which have been reduced to ash, microscopic examination shows that the epi-

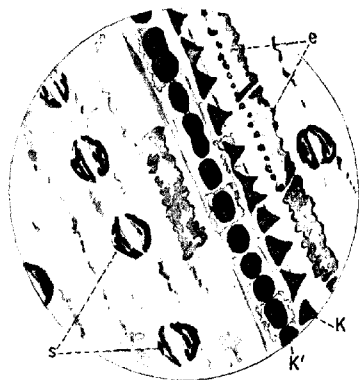


FIG. 15. *Bambusa* sp. Ash-picture of a leaf after treatment of the silicified epidermis with HCl. *s*: stomata; *e*: wavy epidermal cells, many of which are completely filled with silicic acid; *k*: completely silicified epidermal cells. $\times 285$. Original.

dermis is in the form of an ash-skeleton as a result of excessive incrustation with calcium, silicic acid, or with both (Fig. 14). The cell outlines, the stomata and the hairs are so distinctly visible and the tissue appears to have been so perfectly preserved with all its morphological characters that an inexperienced person would think he was looking at a genuine tissue and not merely at its ash. The mineral content of the epidermal tissues, as revealed by many analyses, is much greater than that of the ground tissues. The ash content of the leaf margin, too, is usually greater than that of the

flat portion. Thus, when the total ash content of the leaf amounts to 20% it does not follow that that of the epidermis also is 20%.

If a one-year-old leaf accumulates so much ash material by autumn that the cell walls appear in the ash as a silicified skeleton and reproduce the form of the tissue with exactness, it follows that in a leaf living several years the tissues must gradually become so incrustated, especially with calcium and silicic acid, that normal functioning is hardly to be expected. Certain leaves, as those of the elm, acquire a high degree of brittleness at the end of the first year because of this excessive mineralizing of the epidermal tissue and are easily broken off when withered or dried out.

This striking incrustation with ash materials must provoke disturbances in the functioning of the leaf, and we know that even slight derangements may lead to leaf fall. The autumnal casting of foliage and of the leaf as an individual must certainly be regarded, from this viewpoint, as an adaptation with a particular purpose, because it effects the removal of leaves no longer capable of functioning and provides room for young ones.

Soft succulent leaves, on the contrary, are often so damaged by hail, wind, storm, insects and fungi during only one vegetative period that they can serve their purpose very poorly the second year. We need consider only the leaves of a tree in late autumn, scarcely one of which is seen to be entirely uninjured.

We might raise the question as to how it is possible for some leaves to live two or more years if strong mineralization of the leaf can cause disturbances in its functioning after only one year. Such longevity is possible only when special provision is made by particular adaptation for such long-lived leaves to accumulate and deposit less mineral matter. It becomes necessary, to this end, that they transpire less than do others, and all leaves of several years' duration are actually provided with many sorts of protective measures against transpiration, such as reduced surface, waxy covering, obstruction of stomata with wax (conifers), depression of stomata, thick cuticle, hyperdermal layer, and thickening of the epidermis and cell walls in general. Weakly transpiring leaves of this nature generally contain less ash because the transpiration stream with its dissolved salts is by far more moderate in them than in soft annual leaves.

My contention that the deposition of mineral substances within

the leaf must finally lead to such an accumulation that functional disturbances are introduced, is supported by the correlation which exists between the lesser quantity of ash and the longer life of evergreen leaves. It is supported also by experiments which I have made with two-year-old potted plants of birch and hornbeam kept in very moist surroundings. So long as I cultivated these trees in large sealed glass containers in a cold house, thus inducing very reduced transpiration, the leaves remained alive much longer than on control plants. In the case of the birch, yellowing of the foliage within the damp chamber did not begin until December and leaf fall occurred only in January, while the leaves of the hornbeam remained green until the middle of February and fell only at the beginning of March; the leaves of the controls turned yellow or fell in the beginning of November.

How is it possible in view of all this that the leaves of *Welwitschia* retain life for decades, even up to 100 years? This apparent contradiction is very satisfactorily explained if we recall that the two solitary leaves which the unbranched and turnip-shaped stem of this plant bears, constantly die off at their ends but continue to grow at their bases.

Thus has Nature chosen an effective means of prolonging the lives of evergreen leaves in so limiting the stream of dissolved mineral substances by means of special anatomical adaptations that the leaves store up at a much slower rate the same maximum amount of ash that would render their retention otherwise impossible.

HAIR

We are indebted to Burkhardt²²⁰ for a detailed study upon this subject. It is well known that hairs are manifoldly varied in both structure and function and that their length of life is correspondingly variable. Setaceous hairs are generally long-lived and in the case of soft hairs longevity usually increases with augmented thickening in the walls. The pubescence of fruits and seeds generally falls earlier than does that on leaves and pedicels. Insect-trapping hairs are short-lived, usually dying along with the flowers, and in the case of *Aristolochia*, this takes place even earlier in order to provide exit for pollen-laden animals. Woolly hair also dies early and soon fills with air. The same is true of flight-hairs, as on the fruits

of willow, poplar and many composites. Root-hairs, too, as has long been known, are short-lived.

The longevity of hairs frequently shows a definite relationship with their function. Hairs which soon become filled with air and consequently die are short-lived because they can just as effectively perform the functions of modification of light and protection against transpiration and excessive heat when dead.

Certain functions can be performed, on the contrary, only by hairs which long retain their living contents. Attention may be directed, among others, to the stinging hairs of nettle, to hairs which contain tannic acid as a defense against animals, to hairs secreting resin and volatile oil, and to water-expelling hydathodes. Unfortunately Burkhardt has given no figures of longevity and has thereby left a vacancy which has yet to be filled.

THE DEATH AND LONGEVITY OF TISSUE CELLS

Whenever in the foregoing we have spoken of trees which live for a hundred, a thousand, or for several thousand years, we always think of the tree as a whole, as an individual entity. It must not be forgotten, however, that the organs of an old tree, the leaves and the flowers, have only a short existence, and that the smallest units of the plant, the cells, often live for a much shorter period than the tree itself. Without exaggeration it may indeed be remarked that an old tree consists for the most part of dead cells and resembles a ruin in which only a few of the original rooms are still in use.

How and when does the cell die? In most cases, cells die because their contents have either entirely or for the greater part disappeared. The living substance is destroyed, used up, or has moved elsewhere, and upon disappearance of the protoplasm from the cell, death enters. This is what happens in the pith, the wood and the periderm.

PITH

Let us first consider the pith. It consists, either for the most part or exclusively, of parenchymatous cells which at first contain protoplasm and a nucleus, frequently also starch, chloroplasts or even crystals of calcium oxalate. After a certain age the contents begin to disappear more and more; protoplasm, nucleus and starch are resorbed until finally the cell appears completely or almost en-

purely empty. It then consists only of its wall. The pith of elder, *Sambucus nigra*, of the sunflower, *Helianthus annuus*, of *Aralia papyrifera* and of numerous other herbaceous and woody plants is composed of such empty, air-filled dead cells. Collapse and mutilation of the cells are often associated with this loss of contents in the pith, frequently resulting in cavities of the pith or stem, as in numerous horsetails, grasses, Umbelliferae and Compositae.

The following table upon the longevity of pith cells is taken from the work of one of my students²²⁷ who undertook the investigation upon my suggestion.

As these figures indicate, longevity of the pith is variable, even among closely related plants, and cells of the same pith likewise act differently if they are of different anatomic construction, *i.e.*, thick- or thin-walled. The thin-walled cells usually die earlier than the thick-walled.

Among the woody plants which were investigated, the maximum longevity of pith cells varied between a few months and one to 42 years. Fritzsche²²⁸ has since studied the longevity of pith cells without, however, mentioning the work of Massopust which escaped his attention. He found that homogeneous pith* either remains alive up to formation of heartwood or dies before this process sets in. In birch he found pith that had remained alive for 40 years but in older trunks it had died. If the pith is heterogeneous, it begins to die out first in the internodes and only somewhat later at the nodes.

In certain cacti the pith cells are surprisingly long-lived. As MacDougal²³⁰ has shown, the giant cactus, *Carnegiea gigantea*, which occurs so commonly on the deserts of Arizona, becomes 100 to 150 years old and its pith consists of parenchyma cells which acquire a similar age without losing the ability to divide. MacDougal has also presented²³¹ observations upon the age of cactus cells in *Ferrocactus Wislizenii*. As I have been able to see for myself, this gigantic cactus is of frequent occurrence in the country surrounding the desert laboratory in Tucson where it is of

* Gris²²⁹ distinguishes between homogeneous and heterogeneous pith, the former consisting of living cells with few crystal-bearing elements, the latter, for the most part, of dead pith cells and of living "Markkrone." ("Markkrone" refers to the totality of the primary xylem of the vascular bundle, according to Schneider's "Illustriertes Handwörterbuch der Botanik," Ed.)

PERIODS OF LONGEVITY OF CERTAIN SPECIFIC KINDS OF PITH

| Plant | Nature of pith | Longevity in years | Remarks |
|-------------------------------------|-----------------|--------------------|---|
| <i>Sambucus nigra</i> . | Homogeneous | 1 | Only the pith cells of the upper internodes were still alive in the middle of June. |
| <i>Larix europaea</i> . | " | 1 | Most of the pith cells were still alive the middle of June. |
| <i>Juglans regia</i> ... | Non-homogeneous | 3 | On June 10 the pith showed no chambering and consisted solely of active cells. The thick-walled cells live three years. |
| <i>Robinia pseudo-acacia</i> | " | 5 | The thin-walled cells soon die, the thick-walled live a maximum of five years. |
| <i>Salix Caprea</i> ... | " | 5 | The thin-walled cells die already during the first vegetative period. |
| <i>Acer platanoides</i> . | " | 6 | The thin-walled cells generally die early, but some live a few years. |
| <i>Abies pectinata</i> . | " | 6-7 | |
| <i>Picea excelsa</i> ... | " | 6-7 | |
| <i>Taxus baccata</i> .. | Homogeneous | 7 | The thin-walled cells die very early; on April 27 the current year's shoot was hollow. |
| <i>Rosa canina</i> | Non-homogeneous | 8 | |
| <i>Symphoricarpus racemosus</i> ... | " | 10 | |
| <i>Pinus silvestris</i> . | Homogeneous | 10-11 | |
| <i>Prunus avium</i> .. | Non-homogeneous | 11 | |
| <i>Pirus malus</i> | " | Slightly over 12 | |

PERIODS OF LONGEVITY OF CERTAIN SPECIFIC KINDS OF PITH—(Continued)

| Plant | Nature of pith | Longevity in years | Remarks |
|------------------------------------|-----------------|--------------------|--|
| <i>Syringa vulgaris</i> | Non-homogeneous | 12 | By the middle of June the thin-walled pith cells in most twigs had died. |
| <i>Populus tremula</i> | " | 12 | |
| <i>Viburnum Opulus</i> | " | 13 | |
| <i>Ligustrum vulgare</i> | " | 14 | |
| <i>Prunus spinosa</i> . | " | 14 | |
| <i>Crataegus Oxyacantha</i> | " | 14 | |
| <i>Aesculus Hippocastanum</i> | " | 17-18 | Limit of life in the 20th year. |
| <i>Pirus communis</i> | Homogeneous | Slightly over 18 | |
| <i>Corylus Avellana</i> | Non-homogeneous | 22 | |
| <i>Quercus pedunculata</i> | Homogeneous | | |
| <i>Alnus glutinosa</i> . | " | | |
| <i>Carpinus Betulus</i> | " | | |
| <i>Betula alba</i> | " | 27 | Probably an exceptional case. |
| <i>Tilia parvifolia</i> . | Non-homogeneous | 28 | |
| <i>Sorbus Aucuparia</i> | " | 35-40 | |
| <i>Fagus sylvatica</i> . | Homogeneous | 42 | |

use in many investigations. Among other things, MacDougal could prove that the extraordinarily water-laden trunk, kept in a dry room, could remain living up to six years without access to any water. One plant, when removed from its natural location, in November, 1908, weighed about 38 kg., and on December 7, 1914, its weight was 26 kg. Fully grown specimens are egg-shaped in form, 1.5 to 2 m. tall, and weigh 100 to 225 kg. The greater part of the stem consists of cortex, the central pith being only a few millimeters in diameter. Between these two portions are fibro-vascular bundles which also penetrate through the cortical tissue. Pith and cortical cells remain alive for a hundred years or more. The pith cells attain their ultimate size during the first ten years and show no marked changes in volume during this time. While the cross-sec-

tional area of the cortical cells increases forty-fold during the first decade, in the next hundred years the area is doubled on an average only once. There is a difference between *Carnegia* and *Ferrocactus* to this extent that the pith cells of the former retain their ability to grow and to divide, while the pith and cortical cells of the latter retain the ability to increase in size for a period of a hundred years but lose their power of division.

WOOD

The wood of conifers, aside from pith rays, consists of tracheids and parenchyma cells, and in broad-leaved woods there are, in addition, vessels and libriform fibers. The vessel is composed of a row of cells which lie one above the other and whose cross-walls are soon wholly or in part absorbed. The protoplasm disappears early, and the vessel becomes empty and dies. Death in the wood appears first in the vessel; even before the internode is fully developed the vessel dies. Tracheids, too, live for only a short time, for they also soon lose their contents, become empty and die. The unusually short lives of vessels and tracheids are closely correlated with their functions. They are the means of conducting water and can do so effectively only when they become as empty tubes. The earliest possible liberation from their living contents appears, then, as a practical adaptation to their function. The longest-living elements in the wood are the parenchyma and pith cells and the septate libriform fibers. They conduct and store starch during vegetative periods and constitute a reservoir of various necessary materials in the trunk.

Strasburger²³² has furnished some careful observations upon the longevity of cells in the wood which conduct starch during winter. He has shown that in one 60-year-old Norway spruce living ray cells were found beneath 24 external layers of annual rings. In a 42-year old Scots pine the living elements of the rays extended inward as far as the 28th annual ring and in another specimen to the 36th. In the trunk of a larch the last living element was found in the 32nd ring from the outside, and in another specimen in the 20th ring. In a trunk of *Thuja occidentalis* the rays were found to be alive in their entirety throughout the last 21 annual rings. From this point to the pith the ray cells decreased conspicuously and their starch was replaced by brown masses of resin. In a 26-year old

branch of *Acer platanoides*, living cells were found all the way in to the pith, and in a specimen of *Acer pseudoplatanus* they were alive in 30 annual rings. Parenchyma cells in *Robinia pseudoacacia* remain alive and active for 8 years. A 124-year-old red beech showed living parenchyma and ray cells as far as the 30th annual ring, then in decreasing numbers; isolated cells with starch were found all the way to the pith. Strasburger did not examine further to determine if these starch-bearing cells near the pith were still alive. The presence of starch does not appear to me to be proof that they were living, for it is indeed possible that they became enucleated and that their starch, consequently, could no longer be dissolved.

Further observations on the longevity of parenchyma cells in woody plants are furnished by Schorler.²⁹³ He found the following:

| | | |
|----------------------------------|--------------|------------------------------|
| <i>Taxus baccata</i> | 21-year old | ray cells |
| <i>Pinus silvestris</i> | 35- " | " " " |
| <i>Pinus silvestris</i> | 35- " | " " wood parenchyma cells |
| <i>Picea excelsa</i> | 32- " | " " starch-bearing cells |
| <i>Abies alba</i> | 45- " | " " ray and parenchyma cells |
| <i>Morus alba</i> | 8- " | " " " " " " |
| <i>Ulmus effusa</i> | 14- " | " " " " " " |
| <i>Quercus pedunculata</i> | 18- " | " " " " " " |
| <i>Fagus sylvatica</i> | 15-20- " | " " " " " " |
| <i>Betula alba</i> | 39 & more | " " " " " " |
| <i>Salix</i> sp. | 6- " | " " " " " " |
| <i>Populus alba</i> | 10- " | " " ray cells |
| <i>Populus dilatata</i> | 10- " | " " " " |
| <i>Staphylea pinnata</i> | 8- " | " " " " |
| <i>Sorbus terminalis</i> | 86- " | " " starch-bearing cells |

Fritzsche,²⁹⁴ too, was concerned with the longevity of woody elements and came to the following conclusions:

1. In dicotyledons with genuine heartwood all parenchyma cells, substitute fibers, fiber cells and ray cells remain alive until heartwood formation. The transition from sapwood to heartwood occurs within one to three annual rings, whereupon the parenchyma and fiber cells die first and the ray cells last.

2. Transition from sapwood to heartwood is very rapid in conifers: in one annual ring in the case of *Pinus silvestris*, while in the larch and spruce some elements begin to die already in the first

annual ring. Within the rays a large number of cells gradually perish.

3. In dicotyledonous sapwood all the cells remain alive in some cases until formation of a false heartwood within their midst. Usually, however, the cells die, in part, beginning at the first annual ring, and become filled with infiltration substances.

4. Libriform fibers usually live eight weeks; rarely do they remain alive during the winter though in *Salix* they live until as late as autumn of the third year.

In his investigations on the longevity of pith and cortex cells, MacDougal studied the longevity of parenchyma elements in the wood of *Sequoia sempervirens*.²³⁵ There are two kinds of parenchyma cells in the newly formed secondary wood of this tree, namely, wood parenchyma cells in vertical rows scattered between the tracheids, and ray cells. Both are living and filled with starch in the sapwood.

Upon transformation of the sapwood into heartwood, indicated by a brownish-red coloring, starch disappears from the ray cells. Death and decomposition of the protoplasm are not always associated with this change, however, for these cells, though now in the heartwood, possess a thin plasma-membrane, a distinct nucleus and a large central vacuole. Such living cells can be observed in the heartwood to a depth of 70 annual rings and since the sapwood comprises 21 to 23 rings, MacDougal estimates the age of the ray cells to be about 100 years. Long-lived cells in plants are always parenchyma cells in contrast with the highly specialized cells in the brain and heart of vertebrates. Long-lived cells of *Sequoia* no longer possess the ability to divide and do not function in callus formation and other types of regeneration so common in these trees.

We have, then, both short-lived and long-lived elements in wood. To the former belong tracheae, tracheids, and libriform fibers whose lives are measured only in weeks; in the latter class are parenchyma cells which can live for years and decades. Those of *Sorbus torminalis* remain alive as long as 86 years and those of *Sequoia* as high as a century.

The heartwood, lying within the trunk and frequently distinguished by a darker coloring and definite contents, is usually dead wood, consisting almost exclusively of dead elements and no longer taking part in conduction of sap. The surrounding sap-conducting

sapwood, too, is composed only partially of still living cells, for the tracheae and tracheids function properly as water tubes only in a dead condition. They die early, therefore, while the parenchyma here remains alive for a comparatively long time.

Death of the cells within the body of the tree may come about principally in two different ways. They die either because they become empty or laden with waste products of metabolism, with resin, gum and phlobaphene.

CORTEX

Cork cells are decidedly short-lived. It is characteristic of them, so to speak, that they soon use up their protoplasm and other cell contents, generally fill with air and so perish. Instead of air, other materials may also be deposited in them, *e.g.*, phlobaphene, resins, tannins, *etc.*

If the cork cells do not develop from the epidermis but deeper in the cortex, then all tissues outside the dead cork layer are shut off from conduction of sap and they die. Thus the bark is formed, consisting solely of dead cells.

Little is known concerning the age of lenticel cells.²³⁶

We have previously given considerable data on the longevity of wood elements, but with respect to components of the bast I have found almost no information. Strasburger²³⁷ says that sieve tubes and companion cells in older parts of the trunks of lindens live four years and longer. The emptied sieve tubes carry air. The parenchyma layers in the bast live long, 25 years, until their existence is terminated by cork layers which deprive them of a supply of food. Bast parenchyma in *Aristolochia tomentosa* lives at least 28 years.

It would be a worthy undertaking to supplement these sparse data upon the longevity of the phloem with similar information concerning the various families of plants.

In spite of this dearth of observations upon the subject, it is clear that the death of cortical cells can be attributed primarily to two causes: 1. complete disappearance of protoplasm with resulting emptying of the cell; 2. drying out of the cells through severing of the sap supply by means of cork cells.

STOMATA

Investigations²³⁸ upon the stomata of the giant cactus *Carnegiea gigantea* have yielded the surprising result that stomata on the trunk

attain an age of 100 years, and in spite of this age they remain alive and open and close. This is a conspicuous example of unusually great age in cells belonging to the epidermis.

ROOTS

What has been said of the stem applies equally well to the roots of woody gymnosperms and dicotyledons which increase similarly in thickness. They, too, like the stem, consist of a woody structure which increases every year by an annual ring, and of a cortex covered by a periderm. It is only the pith that is usually wanting.

Death of the tissues in the wood and cortex occurs, *mutatis mutandis*, as in the stem. The conditions obtaining in the still elongating and very young parts of the root merit particular consideration, however. At its apex the root is covered by the so-called root-cap. This consists of parenchyma cells rich in sap which by a partial mucilaginous conversion of their walls spontaneously separate from one another into the layer bordering on the surrounding medium. The cells, thus disconnected from the plant itself, soon die. Here, then, it is neither the using-up nor the removal of the protoplasm which leads to death but merely a separating from the mother plant.

A very short distance back of the root tip arise the unicellular root-hairs, so essential for nutrition, which are in the closest contact with soil particles, cemented together with them, so to speak. They live only a short time, a few weeks, and are constantly replaced by new ones behind the root-tip. According to Schwarz,^{22a} the root-hairs of maize remain fresh for a distance of 20 cm. from the root-tip, while on the more slender roots, the root-hairs die only a short distance from the tip.

Root-hairs are very sensitive to external conditions, especially toward desiccation, heaving out of the ground, transplanting and toward chemical changes in the substratum. Their death can be conditioned by these factors or by the epidermis being removed and replaced by the outer endodermis or by subepidermal cork. Removal of the epidermis also results in death of the root-hairs.

LEAVES

It has already been mentioned that the longevity of deciduous leaves is relatively short, whether they belong to plants which live only a few years or for thousands of years. Very often the leaf dies at the end of the first vegetative period, and not infrequently

still earlier. It has also been discussed in detail how, as a result of transpiration, disturbances must come about from incrustation of the leaf cells with mineral substances which, if continued sufficiently long, eventually leads to death.

Associated with this is the yellowing of foliage which appears in the woods in such magnificent tones of color shortly before the autumn leaf fall and which may be regarded as a symptom of senescence and of approaching death. I have already briefly considered this elsewhere²⁴⁰ with the following comment: "Under normal conditions, yellowing sets in only at a particular age of the leaf. Differences in age of a few days can be a factor in the initiation of yellowing. Yellowing of the foliage usually develops on any branch in an acropetal sequence with conversion first of the lowermost leaves followed by the intermediate ones and finally by those at the end of the twig, the youngest. Though the leaves make their appearance on a twig one after another in spring within two to three weeks' time, differing thus only by slight differences in longevity, the yellowing develops in many cases strictly according to their sequence of appearance.

"Trees which for whatsoever reason burst forth in spring a few days sooner than others of the same species, likewise show yellowing a few days earlier. Vigorous branches which are bent down before sprouting and which, consequently, acquire foliage later than the rest of the tree, retain their leaves in a green condition longer because they are younger. Trees which shed their foliage early because of summer dryness and then acquire new foliage in late summer, remain green until late in autumn. Though these young leaves are exposed to conditions which favor yellowing, they do not change and not infrequently are they destroyed by severe autumn frosts while yet green. All this indicates clearly that at least under normal conditions the initiation of yellowing is generally associated with a particular age of the leaf. Yellowing, therefore, is an indication of senescence."

In referring to my earlier contribution in connection with the microscopic changes which take place during yellowing, I want to call attention to one particularly important change that finally prevents the leaf from functioning normally. I refer to the disappearance of chromatophores and of protein from the leaf. As soon as the yellowing process begins to set in, the green pigment disappears

more or less rapidly, the chlorophyll grains become disorganized and are replaced by yellow oily drops; in many cases, the protoplasmic basis of the grains disappears completely so that the leaf becomes very poor in protein. This is convincingly shown by the method which I have introduced to show the protein of entire organs.²⁴¹ Though the completely yellowed leaf possesses no chlorophyll and often also no chromatophores, it still consists of living cells with protoplasm and nuclei. Such a leaf, however, is no longer able to serve in its natural capacity of assimilating carbonic acid; and because its principal function is destroyed, it is soon discarded. Though completely yellowed it falls while still alive and only after being cast off and dried out or rotted on the ground does it actually die.

FLOWERS

As has already been shown in detail, flowers are relatively short-lived. They fall after fertilization, or, more accurately expressed, certain parts, the corolla, calyx and stamens fall. When such organs are discarded they are usually not dead but still comparatively fresh. They can also fall in a withered condition and in certain cases this withering can occur shortly after fertilization, probably as a result of water removal through neighboring parts of the plant. Here, too, it appears that organs which have fulfilled their purpose and no longer are needed, are discarded in spite of their still being alive. Physiological interest attaches to the manner in which many ephemeral flowers die, for example, those of *Tradescantia virginica*. The flowers open early in the morning and by afternoon of the same day the violet petals begin to curl up into a juicy mass and the protoplasts become pervious to the violet cell sap and die. It is not known at present what causes this premature death of the petals or what causes the plasma membrane to become pervious to the dissolved anthocyanin pigments.

POLLEN

The longevity of pollen²⁴² has been studied under various conditions for 50 different angiosperms. Air-dry preservation has been found the most suitable in this work. The pollen of *Typha* has been found to be the longest-lived, retaining its germinating capacity after 158 days to the extent of 56%. After 336 days the ability to germinate had not entirely disappeared.

ISOLATED CELLS

The life of the cell can be conspicuously curtailed by removal from its tissue, with subsequent cultivation. Haberlandt²⁴⁸ was the first to attempt such isolation of cells from organs, *e.g.*, from leaves, and then to preserve them in a living condition. Several investigators followed him, Bohiloff-Preisser, Thielmann,²⁴⁴ Winkler, and Küster,²⁴⁵ without any of them having succeeded in keeping cells alive long which had been separated from one another, to say nothing of bringing about active growth or even formation of an organ.²⁴⁶

Thielmann and Berzin²⁴³ investigated changes in the osmotic value of cultivated cells and determined the longevity of isolated cells in various nutrient solutions. The experiments were performed with thin sections which consisted more or less of mesophyll cells in addition to the epidermal and guard cells, or they contained mesophyll cells exclusively. The longevity of mesophyll cells from monocotyledons amounted to 11 to 12 days at 16° to 17° C. in water and in the case of dicotyledons, to 7 to 24 days. Guard cells lived longer under similar conditions, about 19 to 42 days. The longevity of mesophyll cells was dependent, aside from external conditions, upon the presence of the epidermis and of "nerve parenchyma";* the closer the anatomic nature of the cultivated sections approached that of the normal leaf, the longer did the mesophyll cells live.

Guard cells possess a greater longevity than other cells in the leaf, approximately 18–50 days. But even this period is relatively short in comparison with that of the entire leaf and from this it is apparent that isolated bits of tissue as well as isolated cells are shorter-lived than the leaf itself.

SUMMARY

In summarizing our observations on the age of tissue cells, we can say in conclusion that tissue cells can attain different ages according to the organ and the tissue of which they are a part, and according as they belong to plants which live for one, many, hundreds or thousands of years. They can last for days, months,

* "Nerve parenchyma," according to Schneider's "Illustriertes Wörterbuch der Botanik," applies to the chlorophyll-less cells, rich in protoplasm and possessing large nuclei, which accompany the end tracheids in the vein endings of broad leaves.—E. H. F.

or many years, but in comparison with the great age of many species of trees, the longevity of their component cells is relatively short. The oldest living cells yet found are the parenchyma and ray cells of wood, attaining a maximum age of about 80 years; while those in the cortex and pith of certain cacti can live for a century and more.

In a thousand-year-old linden or in a sequoia of several thousand years the oldest living cells, at best, are not much over 100 years of age. Their functions are not necessarily concluded at their death, for the dead cells of the wood provide the rigidity of the trunk and thereby render the tree an important service.

CHAPTER IV

THE MEANS OF PROLONGING THE LIFE OF PLANTS

It is not difficult to understand that man, who alone among all living organisms knows that he must die, should have early attempted to find some means by which his life might be prolonged. To most of us death appears as something horrible, to many as something to be feared, and because of this it is not surprising that since time immemorial man has sought various means of rejuvenation and of postponing senility. The mystical drink of immortality among the Chinese, the elixir of noted magicians and physicians, the macrobiotics of Hufeland²⁴⁷ founded upon common and medical experiences, the claims of Metschnikoff²⁴⁸ established upon biological facts, and the rejuvenation experiments of Steinach and Voronoff may be only mentioned here as illustrations. The problem of prolonging man's life has thus already been considered in its practical aspects and in recent times has been exposed to animated discussion in scientific writings and daily newspapers.

It is surprising, however, that the matter of prolonging life among plants has not been extensively considered. In the larger works upon plant physiology this problem, so very significant from a general biological viewpoint, has occupied conspicuously little space, though many studies have already been made upon the subject. It appears to me worthwhile, in view of this state of affairs, to present this interesting problem in a separate chapter, on the basis of previously known facts and my own observations, and thus render a possible service to the field of general biology. There are, as a matter of fact, various devices by which the longevity of plants may be prolonged. We shall examine them and in so doing I shall rely for the most part upon a summary of the work of others as well as upon my own which already embraces a number of years.²⁴⁹

1. EXCLUSION OF ALL ADVERSITIES

Whenever reference is made to the prolongation of life among plants, two different ideas may be involved, either the greatest possible postponement of death within a normal life-span, or a prolongation of life beyond its normal period.

The first case is of little interest, for it is self-evident that by preservation of a healthy condition through careful avoidance of injury, a plant may be kept alive until its natural end. Adversities which tend to curtail a plant's existence are abundant, and I need refer, among many others, only to lack of nutrition, light, water and pure air, and to the countless parasites within both the plant and animal world; there are also extreme heat and cold, lightning, hurricanes and floods. All these factors can shorten the period of longevity, and by avoiding them life can be extended. In this sense we may speak of the macrobiotics of plants just as we have done with respect to man since the time of Hufeland.

In addition to this art of maintaining plants in a healthy condition during their normal span of life and up to their natural death, we are interested also in extending their lives beyond the normal period, for this gives us a deeper insight into various phenomena of plant life, especially into the nature of old age and its associated decadence.

2. TEMPORARY REMOVAL OF THE INDISPENSABLE CONDITIONS OF LIFE

Active life takes place only when certain external conditions are fulfilled, namely, when there is provision of oxygen, of a particular temperature, and of a supply of nutriment. If one of these requisites be lacking, active life ceases, and if the plant is capable of enduring this abnormal condition for any protracted period it enters a state of apparent death. A dried-out kernel of corn, for instance, exhibits neither growth, assimilation nor any other type of activity, and shows no indication of being alive. If it is placed in moist earth, however, and is in a position to absorb water under favorable conditions of temperature, it germinates and continues to grow, and the resulting plant flowers, fruits and dies the same year. Were the kernel to be deprived of water for a longer period, perhaps for several years, the life of the inclosed embryo would thereby be prolonged a corresponding number of years. Viability of the seed persists for only a certain length of time, however. The germinating capacity of seeds of barley, oats and wheat preserved for ten years in a dry condition amounts to from 70% to 90%, and the seeds of the sensitive plant, *Mimosa pudica*, are still capable of germination after 60 years. Under normal conditions the corn embryo placed in moist soil immediately begins to germinate and

in the same year completes its development and dies as a fully matured plant. Prevention of germination through removal of water, on the other hand, can postpone the development for years and can considerably prolong the latent life of the embryo. So we see that life can be almost completely arrested and again resumed after some time by provision of necessary conditions, just as a clock can be stopped by checking the pendulum without permanent injury to the time-piece.

The same situation prevails with respect to many bacteria, fungal spores, mosses, bulbs, bulbils and root-stocks. They can all endure desiccation for months, often years, and then under suitable conditions can recover from their dormancy and complete their life cycle. Also, according to Nestler's investigations,²⁵⁰ there are some spore-forming bacteria, *Bacillus vulgatus*, *B. mycoides* and *B. subtilis*, which can withstand drying-out for decades and can be kept alive for at least 92 years.

Development can be postponed, moreover, not only by removal of water but as well by the exclusion of other basic conditions such as favorable temperature and a supply of oxygen and food material. If a small tree of elder, for example, is placed in an ice cellar after leaf-fall in autumn and kept there for an entire year at a temperature slightly above the freezing point, sprouting is hindered and vegetative growth artificially held back. The longevity of the flower primordia inclosed within the buds, which under normal conditions would develop in spring and be discarded after flowering in separate parts as corolla and stamens, is thus prolonged until such time at which sprouting is encouraged by transferring the plant to a favorable temperature.

In all these cases there is involved an interpolation of a period of latent life within the developmental cycle of the plant, whereby the life of the plant itself or of some part is extended.

3. PREVENTION OF FLOWERING AND FRUITING

There is frequently cultivated in our conservatories a certain plant which has received the name of "the hundred-year Aloë." This name is without justification, however, for the plant is not an Aloë; it is properly known as *Agave americana* and, moreover, it usually does not live for a hundred years. In its native habitat in Mexico it is of economic importance, for it exudes a considerable quantity of sweet water from the wound created by cutting out the

entire young inflorescence;²⁵¹ upon fermentation this exudate furnishes 'Pulque,' the national drink of the Mexicans. In Mexico the plant flowers, fruits and then dies after eight to ten years' growth. In an unfavorable climate, however, such as prevails along the Italian and French Rivas or on the Dalmatian coast, where the plant has become acclimatized, or in our more northern conservatories, it requires, according to the total amount of light and warmth which it can receive, 20, 40, 50 and even 100 years before it is prepared to develop its large inflorescence and mass of fruit and then to die. This undoubtedly accounts for its being called the 'century plant.' Thus we see that postponement of flowering through climatic factors considerably prolongs the life of these plants.

It is well known, furthermore, that there are certain plants which flower and fruit only once during their lives and then conclude their cycles, viz: chickweed, *Stellaria media*; speedwell, *Veronica hederifolia*; and mercury, *Mercurialis annua*. There are also others which produce fruit twice, occasionally, or frequently before they perish, as is true of most woody species. Hildebrand²⁵² designated the former as monocarpic, the latter as polycarpic. Among monocarpic forms, including *Agave*, complete exhaustion of the plant occurs subsequent to flower and fruit formation. During the period previous to flowering in the *Agave* there is a constant production of food by the huge leaves which, as soon as the plant reaches its ultimate size, is stored as reserve material for the future large inflorescence. Before the necessary quantity is accumulated the plant does not flower. In its native home this goal is attained relatively early, in eight to ten years, but in our conservatories not until many years later, for under the unfavorable climatic conditions which obtain under such circumstances, assimilation proceeds much more slowly and the necessary amount of material requisite for flower and fruit formation can be accumulated only during a much longer period of time. Prolongation of life in this plant is thus associated with postponement of flowering, for the termination of life is bound up with fruit production and with the associated complete exhaustion of the vegetative organs. All those factors which tend to protract flowering contribute also toward extending the life of the *Agave*.

Dofflein²⁵³ applies the name "metabolic-death" (Stoffwechselfeld) to the perishing of *Agave* or *Corypha* subsequent to flowering and

fruit production. I do not regard this designation as appropriate, however, for it does not express the true nature of the matter. Metabolism occurs in every active living cell, in the young cells as well as the old, and such metabolic processes certainly take place in a flowering *Agave* or *Corypha*. They are processes which are tied up with the gradual death of the plant, for all the reserve materials which these plants store up in the course of years are mobilized within a short time for flowering and fruiting purposes; all of which results in marked increase in metabolism. The essential feature of this kind of death is complete exhaustion of the stored material, for the reproductive organs and the developing flowers and fruits draw upon the valuable food materials to such an extent that nothing remains for the other organs, and they perish. Therefore, it is more fitting to apply to this state of affairs and type of death the term 'exhaustion-death' (Erschöpfungstod). The yellowing leaf of autumn, too, dies finally from exhaustion because the chloroplasts lose their proteins, disorganize and thereby are deprived of their natural function of assimilation.²⁵⁴

In his interesting treatise on the "hunger-death" of man and animals, Pütter,²⁵⁵ too, arrives at the viewpoint that when planarian flat-worms are reduced by hunger to about 1/300 their original size, finally succumbing to hunger-death, or when fresh-water polyps (*Hydra*) show only 1/200 the volume of fresh specimens as the result of withdrawal of food, exhaustion is to be regarded as the cause of death. Among mammals, according to Pütter, hunger-death is attributable to the injurious effects of metabolic products which are neither rendered ineffective nor excreted. A sort of autotoxication thus develops which I assume takes place also in plants. It would be worthwhile to make hunger investigations upon plants and to investigate the accompanying morphological, physiological, histological and chemical relationships, concerning which very little is known at present.

Doflein has called attention also to the phenomenon of sudden death (Shocktod) as a special kind. The drone of the honey bee is subject to such a fate, for it dies almost immediately upon copulation. The same situation is true of ants, according to Doflein. Among plants, however, such sudden death is unknown, for there is always a certain period of time between the consummation of reproductive processes and the death of the organism.

Let us consider the commonly cultivated *Roseda odorata* of our gardens which concludes its developmental cycle under prevailing conditions within one vegetative period.



FIG. 16. *Roseda odorata*. Extension of longevity through prevention of flowering. Three-year-old plant cultivated as a small tree. Original.

If the seeds are sown in spring, the plant flowers and fruits during summer and dies in the fall. If we suppress its flower formation, however, we are enabled to maintain the plant as a small crown-bearing tree for two or three years. In order to achieve this effect all flower primordia and lateral shoots are removed from the young seedling immediately upon their appearance. As a result, the main stem becomes longer than ordinarily and can be made to grow one half to two meters tall; as soon as it has attained the desired height, the terminal shoot is removed, and the lateral shoots but not the blossoms are permitted to develop. By repetition of this procedure a much-branched crown can be acquired. It is entirely up to the experimenter whether or not the plant shall flower; if he suppresses flower formation by repeated removal of any buds that may appear, the life of this ordinarily annual plant can be extended for several years. By this practice, which I have often pursued myself, the stem grows considerably in thickness and becomes

woody, thus best serving its purpose of providing water and nutrient salts to the crown.

In order to secure a fine lawn in the course of several years without repeated sowing of seed, the turf is frequently mowed during the year. In this way, the grass, particularly rye, is prevented from flowering but induced to produce new lateral shoots which again are sheared to prevent their blossoming. By repetition of this practice a vegetative growth of the turf is secured over a period of many years. In a similar manner the life of *Draba verna*, *Veronica arvensis*, *Petunia* and *Lobelia erinus* can be prolonged. Because of its abundantly produced blue flowers, this species of

Lobelia is a favorite bedding plant. If the variety known as 'Kaiser Wilhelm' is seeded in January, plucked in March and transplanted in the open, it blooms from June to July and then turns yellow and dies. If it is clipped before the first flowers, however, it produces new shoots, and if these are again sheared before they flower, such plants may be kept flowering until autumn, and certain species may be kept alive over winter. *Petunia* behaves likewise, in my experience, and I have no doubt that other annuals can be transformed by suppression of flower formation through cutting and corresponding cultivation to plants of two years' longevity and longer.



FIG. 17. *Lobelia erinus*. Extension of longevity through prevention of flowering. The plant on the left died in August after blossoming; the one on the right was twice trimmed short during summer, in order to prevent flowering, and was still alive in December.

In an old but very informative work by Reichart,²⁵⁶ I find the following account in the part dealing with the Vienna wall-flower. "If by always removing the buds we prevent flowering in the second year of a stock which by nature is not inclined to produce lateral shoots, leaf-bearing lateral branches will then arise at the apex. If we permit only the most vigorous of these to remain and remove any blossoms which it may be inclined to produce, then by thus allowing only the most vigorous shoot at the apex to develop we can produce quite a tree. If we wish such a plant to

flower in the third year or even later we do not disturb later lateral shoots which then give rise to fine flower clusters."

Finally, there is a group of plants which ordinarily conclude their development within one vegetative period and then perish. If we sow their seed in autumn, however, and allow them to over-winter, they do not flower until the succeeding year and in this way become so-called biennials. *Matthiola*, *Cineraria cruenta*, species of *Calceolaria* and others are in this class.

Thus we note that in all these cases death is deferred and life thereby extended through a retarding of flower formation.

4. PREVENTION OF POLLINATION AND FERTILIZATION

In the foregoing we have been constantly concerned with life extension of the individual as a whole, but it can readily be demonstrated that the longevity of single organs can also be curtailed or extended.

Upon fertilization certain changes occur within the flower which ultimately lead to fruit production; the egg-cell develops into the embryo, the ovules into seeds and the enlarging wall of the ovary into the pericarp. Perianth segments and stamens are discarded as soon as the flower has attained a particular age, and in certain plants this happens very suddenly, sometimes surprisingly soon after pollination or fertilization. Longevity of the flower can thus be very variable, either shortened through pollination or prolonged by postponement of it.

This influence is frequently noted in certain orchids. The flowers of *Cattleya*, for instance, wither within a day after pollination and then dry up, and it is particularly striking among those whose blossoms enjoy considerable longevity. While unpollinated flowers remain fresh for one or two months, those that are pollinated wither in one or two days. Fitting²⁵⁷ found some other very instructive cases in this respect. Receptive flowers of *Geranium pyrenaicum*, for example, shed their petals as the result of pollination within the amazingly brief period of about one to one and a half hours, and those of *Erodium Manescavi* after only 40 to 60 minutes. Fitting saw the flowers of *Borago* fall two and a half to seven hours after pollination.

On the other hand, the longevity of many organs, as the ovary, ovules and peduncle, can be extended as a result of fertilization, for when the flower is not pollinated and fertilized the entire blossom falls.

5. EXTENDED PERIOD OF FUNCTIONING

It is possible in many cases to extend the functioning period of an organ beyond its customary span of time and thus prolong its life. The leaf of *Begonia Rex*, for example, ordinarily does not become more than one year old in our greenhouses, but I have often succeeded in keeping the petiole alive for two or three years in the following manner. A fully developed leaf with a petiole is

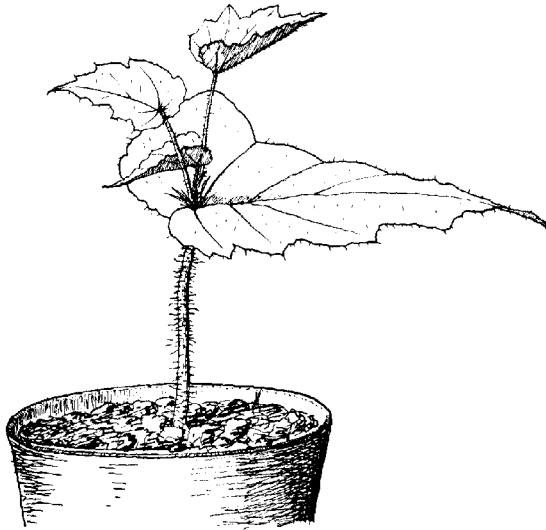


FIG. 18. *Begonia Rex*. Leaf-cutting. The petiole remains alive much longer when the blade develops a shoot. Original.

inserted with the base of the stalk in moist sand and left there until it has formed roots. The rooted leaf is then transferred to a flower pot and further cared for with the petiole supported by a small stake. Shoots arise from the blade after some time and one of them, preferably one breaking out in the neighborhood of the junction between blade and petiole and representing, as it were, a continuation of the petiole, is selected for further development, while the others are removed. Under these conditions the stalk of

the mother-leaf assumes the rôle of the stem (Fig. 18). The young shoot draws up water and nutrient salts which must pass through the petiole, thereby nourishing the latter and maintaining it in a functioning condition. It remains alive much longer, consequently, than it would if it functioned merely as a leaf-supporting structure. Kny,²⁵⁸ too, converted the petiole of an isolated leaf from the same species into the bearer of a leafy individual, and discovered, moreover, that the vascular bundle of the petiole increased considerably in circumference as compared with that of a normal petiole.

Winkler²⁵⁹ secured similar results with the scrophulariaceous *Torenia asiatica*. When the leaves of this favorite conservatory plant are inserted by their petioles in moist sand and have rooted, they soon form several or even many shoots which can arise at the base of the petiole, on the petiole itself, or on any part of the blade. If all the sprouts except a single one on the lamina are removed, the petiole is readily converted into a part of the branching system to such a degree that it serves as the axis of the shoot. By suitable technique, Winkler was able to produce thickly foliated specimens 30 to 40 cm. tall upon the leaf. One individual bore 36 well developed pairs of leaves on the main and lateral axes as well as flowers, many of which produced fruits with numerous viable seeds.

This interesting culture of a relatively large plant with flowers



FIG. 19. *Aucuba japonica*. Rooted leaf-cutting. Original.

and fruits upon a petiole as a base leads to two important deductions, first, that the petiole, in continuing to function for a long time, experiences a most significant anatomical transformation by becoming a stem, and secondly, that its longevity is extended considerably beyond the normal. Winkler regarded the augmented water-conducting capacity of the vessels as the basis of increased cambial activity and abnormal longevity of the neighboring cells.

We have now considered two examples in which leaves are capable of developing shoots from their blades. Such cases are rather rare. It often happens, however, that leaves produce roots but not shoots. Those of *Hedera Helix*, *Aucuba* (Fig. 19), *Camellia*, *Piper* and others develop a strong root-system and, because they continue to assimilate but do not entirely use up the assimilates, they become unusually thick and older than they would in their natural position as part of the mother-stock. Potato leaves which Knight planted in pots under glass during July and August formed tubers and lived until winter. Mer was able to keep leaf cuttings of ivy alive four to five years and Carrière cultivated a leaf of *Hoja carnosa* for seven years.²⁰⁰

De Vries²⁰¹ records an interesting case of prolonged longevity in a pedicel of *Pelargonium zonale* which developed a leaf bud at its apex and, though otherwise annual by nature, it was thus enabled to live on for years and to acquire considerable girth. Toward this end de Vries severed the stem directly above the insertion of the pedicel and was able to keep it alive for three years, three times as long as it would have lived under normal conditions. During this prolonged period of longevity the pedicel became much thicker and surrounded with cork, and it underwent other anatomical changes which enabled it to play the rôle of a stem.

The same author noted also that galls, which occur on inflorescences and leaves, increase the life activity and thickness of these organs through the nutritional stream which they require for their development and upon which they draw from adjoining tissues. The male catkins of the English oak, for instance, fall shortly after flowering, but if they bear galls of species of *Andricus* they remain alive much longer.

Green deformities frequently occur on the male catkins of willow (*Salix alba*) as the result of punctures by plant lice and mites. Such green catkins often grow ten centimeters long, bearing very pubescent leaves, and the axes, which become very woody, do not fall.

The axes of male inflorescences on many plants, furthermore, remain alive longer than normally if they happen to bear an occasional pistillate flower which becomes fertilized: in fact, as long as the female inflorescences, while the axes of normal male inflorescences die off immediately after pollination. This is the case in

Carex, hops, nettle, maize and other plants. Their longevity does not extend beyond one summer, however.

MISCELLANY

We can often observe an extension of life in the cells of yellowing or yellowed leaves which are infested by certain insects or fungi, and for interesting notes concerning this topic we are indebted to Richter²⁶² and certain other investigators, as Cornu, Kochs, Cavara, Tubeuf and Küster. When autumnal yellowing of the foliage of *Acer Pseudoplatanus* sets in and the yellowed leaves are cast from the twigs, there remain in them green islands which are bordered by perforations and sharply distinguished from the chlorotic surroundings. Every one of these green islands contains a tiny green worm and a deposit of its excreta. The epidermis on the lower surface appears detached and forms a membrane over the entrance to the cavity. In freshly fallen leaves the green chlorophyll-bearing parenchyma fills the entire cavity up to the ring-like area where the insect is eating. The grub then eats away the green parenchyma in a circular fashion progressively inward from the circular border of the cavity.

We can see such green islands also in yellowed maple leaves

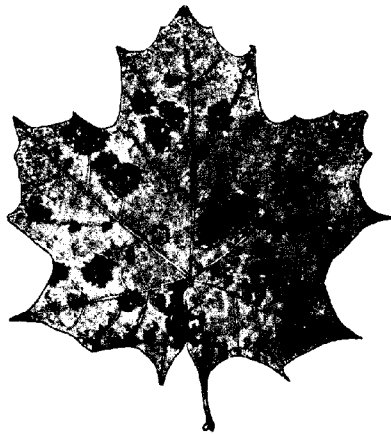


FIG. 20. *Acer platanoides*. Yellowed leaf with green (dark in the picture) spots infested with a fungus. Original.

when they are infested by the fungus *Phyllactinia guttata*. The tissue remains green only in those spots where the fungus has abundantly penetrated, while the fungus-free surroundings become chlorotic. I have often noted this on leaves of *Acer platanoides* in the neighborhood of Vienna (Fig. 20).

According to Werner, the grubs which live in maple leaves are a form of *Lithocolletis*. On the yellowed leaves of poplar and oak Richter also found green areas surrounding cavity entrances, the persistent green color of which was attributable to the excrement of a nepticulid. According to Richter, yellowing does not develop in these spots because the decomposition products of the chlorophyll can not be removed since the translocation stream is interrupted. Wherever the translocation stream is uninjured, this author claims, there is an excretion of certain materials through the animal or, in the case of fungal spots, through the fungus.

Stahl²⁶³ has shown that when leaves which are about to turn yellow are cracked or partly cut through, they remain green longer above the crack or incision than in parts below the injuries. Particular interest attaches to those experiments in which he shows that circular green areas stamped out of leaves on the verge of turning yellow, long remain green, while yellowing appears in other parts of the blade.

All these investigations show that in those regions where chlorophyll is retained longer because of interrupted conduction of decomposition and assimilation products, there is an accumulation of these products which induces better nourishment of the cells and resultant life extension.

Carara reports, furthermore, that the leaves of *Quercus castaneaefolia* in the botanical garden at Naples which were punctured by a plant louse not only remained hanging on the twigs for a long time but also retained their green color, as contrasted with uninjured leaves which turned yellowish or brownish-yellow much earlier.²⁶⁴

Küster²⁶⁵ makes the following observation of an interesting case in which the cells of beech leaves were rendered longer-lived by a gall-producing insect: "Those leaves which are infested with *Oligotrophus annulipes* . . . long remain green at points above the galls, while other parts soon become yellow or brown and shed their leaves. The galls act as a stoppage in the conducting elements and

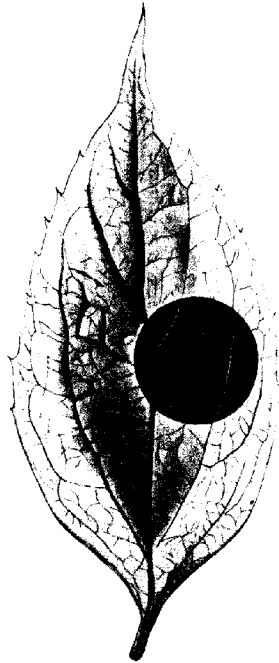


FIG. 21. *Philadelphus grandiflorus*. The circular area stamped out of a green leaf about to turn yellow remains green while the other parts change color. From Stahl.

their effect is similar to the incisions which Stahl made in the veins of his material when regions of the blade above the cut remained green while other parts turned yellow. The boundaries between the yellow and green portions of the blade are no less sharp in the beech leaves infested with *Oligotrophus* than in the *Ginkgo* leaves operated upon by Stahl."

In the same article Küster makes mention also of cases in which certain parts of the leaves remain green abnormally long without any blocking of the bundles being visible to the naked eye. This is exemplified by the yellowing leaves which one sees here and

there on walnut trees. When bearing galls of *Eriophyes tristatus* var. *erinca* they remain green and continue so after leaf-fall.

I have often observed more or less numerous circular or ellipsoidal flecks of deep green with a whitish center on the yellow rinds of lemons which come into the markets of Vienna. The white spot represents a scale insect which influences the neighboring cells in such a manner that the tissue of the rind encompassing the puncture remains green. I dare not say without special inquiry into the matter whether the longer retention of chloroplasts is caused by wound hormones of the injured cells, by secretions of the insect, or by more abundant supply of nutrients to the wounded area.²⁶⁶

It has already been noted that green spots can be caused by fungi in yellowed maple leaves. Cornu²⁶⁷ has cited several examples of this and remarks that maple leaves are frequently infested on their lower surface by *Erysiphe guttata*, and that in autumn when the leaves turn yellow and fall, the areas infested by the fungus, even on fallen leaves, remain green for several weeks.

Cornu made similar observations on the leaves of birch, apple and mountain ash where the green flecks were occasioned by *Cladosporium dendriticum*; also in cabbage and the vine where *Cystopus candidus* and *Peronospora viticola* were the causative agents, respectively. In all these cases the fungus so affects the surrounding tissue, though it is a parasite, that the cells retain their chloroplasts and general activity. This effect strongly recalls the influence of bacteria and of hyphomycetes upon bacteria, as is displayed by the following observations of my own.²⁶⁸ "A plate of nutrient gelatine with a great many thickly clustered colonies of *Bacterium phos-*

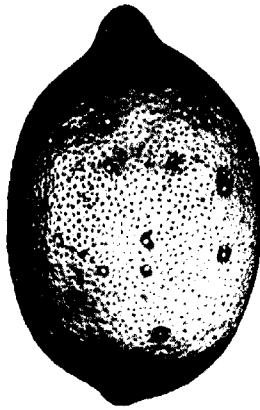


FIG. 22. A ripe, yellow lemon with green (dark in the picture) flecks caused by punctures of scale insects. Original.

phoreum glows markedly during the first days and then because of lack of nutrition the culture begins to diminish in phosphorescence. If the culture is then exposed for a few moments so that it becomes contaminated from the air, small isolated colonies of *Penicillium*, *Aspergillus* and various bacteria usually develop the following days. Observed in the dark, almost every colony together with its immediate surroundings appears as an intensive light field against a dark background. *Penicillium* and the other mentioned fungi peptonize the gelatin and thereby alter the substratum so that the requisite nourishment for light production is present which, entering the bacteria, makes such production possible. Areas of light are frequently followed by regions of growth. So, not only are fission fungi and yeasts able to influence the luminescence of light bacteria, but the higher fungi can do so also by creating suitable conditions for luminescence through certain alterations in the substratum." Similarly, the fungi can influence the tissues which surround them in the green islands of yellowed leaves, either by supplying the neighboring cells of the host with certain secretions or by obstructing removal of assimilates and rendering the latter, so far as they are not utilized by the fungus itself, at the disposal of the surrounding cells. It is possible also that the fungus serves as a focal point of nutrient materials. All these circumstances serve to promote life's energy and longevity.

It may be added, finally, that the death of many plant parts or of the entire plant can be postponed for some time through the following technique. If certain fruit trees which sometimes shed their flowers and fruits prematurely, are girdled, *i.e.*, if the bark is removed from the trunk or a branch in the form of a ring, the organic materials manufactured in the leaves are blockaded by the girdle wound from traveling downward, and since they can not be removed any farther they accumulate above the wound. This accounts for an unusually favorable nutrition of the flowers and young fruits and prevents their being shed. In these cases nutrition accounts for life extension.

Grafting, too, can be of influence. When grown from a seedling, *Pistacia vera* can attain a maximum age of 150 years, but when improved by grafting upon *P. Terebinthus* it may become 200 years old; upon *P. Lentiscus* it lives for only about 40 years. A normal

apple tree, *Pirus malus*, can be 200 years old, but when grafted upon *Malus paradisiaca* it lives for only 15 to 25 years.

It has also been demonstrated through the investigations of Lindemuth²⁶⁹ that annual shoots of herbaceous shrubs and annual plants themselves can be made longer-lived by grafting upon woody forms. Of particular interest in this connection was the experiment by which he cultivated a shoot of the perennial *Abutilon Thompsoni* on the herbaceous annual stem of the malvaceous *Modiola caroliniana*. The *Abutilon* scion sprouted so vigorously after the grafting that it soon came in contact with the glass of the conservatory and had to be trimmed repeatedly. It lived in this association with its stock of *Modiola*, ordinarily an annual herb, for three years and five months and the longevity of the annual *Modiola* was thus extended about two and a half years. It would be very worthwhile if this experiment were repeated a number of times to determine whether or not anatomical alterations go hand in hand with this extension of life and if it would not be possible by careful manipulation to preserve the annual *Modiola* as grafting stock still longer than in the case cited.

An autonomic resting period of about three months, from September to December, is peculiar to the winter buds of *Hydrocharis Morsus ranae*, a period which heretofore could not be notably abbreviated by the customary forcing methods. Wisniewski²⁷⁰ has shown that these buds are able to sprout after their resting period only in light, and Simon²⁷¹ discovered that if they are kept in the dark they can be maintained in a resting condition for years, even for four years and perhaps longer, and their longevity thereby prolonged.

With respect to extension of life in cotyledons, I have made the following observations. If we permit a seed of *Phaseolus multiflorus* to germinate and continue to cultivate it in light, then the cotyledons, which at first are abundantly filled with reserve materials in the form of starch and protein, gradually become depleted, for the reserve materials are utilized in the development of the root system and of the first leaves. After two to four weeks and according to growing conditions, they shrivel completely and dry up if in dry soil, or they decay if on moist soil. Under normal conditions they are active for a relatively short period, generally only about three weeks. The active life of these bean cotyledons can

be extended for several months, however, if their depletion of reserve materials is prevented and if, in addition, provision is made that they can assimilate plentiful quantities of carbonic acid. I have accomplished this easily by early cutting away the epicotyl at its base where it arises between the two cotyledons and by similarly removing upon their first appearance the shoots which develop in the axils of the buds. After this operation the cotyledons soon begin to turn green in the light and, though the decapitated plant produces a strong root system, the cotyledons not only retain their tension and high turgidity but wax noticeably larger than they were. Van Tieghem²⁷² noticed that isolated cotyledons of *Helianthus annuus* and of other plants developed roots and could grow larger and turn green. Probably because he did not pursue the experiment sufficiently long, he failed to observe that thus isolated they lived much longer.

The fact that the cotyledons of my plants upon which I operated thus grew and remained unshriveled, in spite of their developing a strong root system, is to be accounted for, not only by their possessing a large amount of reserve materials, but also by their augmenting this supply of building material through carbonic acid assimilation. Obviously, more is assimilated in the light than is actually represented in the roots. This is apparent also from the fact that the hypocotyl of the decapitated seedlings acquires an amazing thickness, two to three times that of the normal organ.

The decapitated seedling does not know what it should begin to develop with the accumulated nutrient material and therefore appears forced to make repeated attempts to produce new buds from the remaining tissue of the axillary buds which have been removed. New buds develop a few days after these are removed, and this regenerative process can be repeated as often as the adventive buds are lifted. The cotyledons themselves can not produce any foliage buds.

While I thus saw to it that the reserve and newly formed materials were only slightly removed but always replenished through assimilation, the deep-green seed-leaves remained alive for several months (4-6), wholly contrary to their customary behavior, and in full vegetative activity.

Under ordinary circumstances the cotyledons become exhausted in a relatively short period because they place all their reserve ma-

terials at the disposal of the growing plant. In my investigations, on the other hand, they were nourished *beati possidentes* by reserve materials and as carbonic acid-assimilating organs in a very marked degree and this abundance of food materials kept them alive surprisingly long. But their hour comes too, though later, because they are richly filled with reserve materials, and they begin to decay and die, sometimes during the process of yellowing.

Similar to the behavior in the scarlet runner is that of the cotyledons in *Helianthus annuus*, *Ricinus communis*, *Fagus sylvatica*, *Impatiens parviflora*, *Mimosa pudica*, *Acer* sp., *Pisum sativum* and *Cucurbita Pepo*. In all these there is a more or less considerable increase in width and thickness, frequently also an intensive greening, and hand in hand therewith a conspicuous prolonging of their lives, which may be from three to seven times the normal period of longevity. In these cases extraordinary nourishment undoubtedly is the cause of prolonged life.

Just as the life of the plant or of its organs can be extended by definite experiments, likewise can it be curtailed. Among varieties of corn we distinguish short-lived summer forms and long-lived winter forms. Under natural conditions winter rye lives about ten months, summer rye only four months. If we seed out the winter rye in spring, contrary to custom, it does not flower until autumn. It completes its growth up to fruit formation also in spring seeding, however, if its "cold requirement" is taken into consideration by exposing the seedlings to cold, either immediately after their emergence or at some time after seeding. The longevity of the winter crop is thus markedly shortened by two to three weeks' influence of winter temperature (Gassner, G., 1918).

Pater²⁷³ was able to convert biennial medicinal plants into annuals. If the leaves of *Conium maculatum*, for example, are mowed early in their first year of vegetative growth, the plants sprout vigorously and produce flowers and fruits the first year. As a result of mowing, ordinarily biennial plants thus behave as annuals and produce no more shoots the second year. This has practical significance, for it shows that in one year we can obtain what normally requires two years. Dupuy²⁷⁴ says that the longevity of annuals at the seashore is only one-fourth to one-sixth as long as that of the same plants farther inland.

In many cases, shortened longevity can be secured also by grafting. If it is desired to cultivate the apple as a dwarfed plant, it is grafted on *Malus paradisica*, in which case it will attain an age of only 15 to 20 years, whereas a normal apple tree lives up to about 200 years.²⁷⁵

REVIEW

There is no doubt in view of our foregoing observations that the life of a plant as well as that of its individual parts may be prolonged in many cases and by various means. We want to inquire now as to what the causes are which lead to this life extension and whether this prolongation achieved in many different ways is not to be attributed in the last analysis to just a few fundamental causes.

The situation is certainly clear in those cases where life extension is secured by a suppression of active life, as in assuming a state of apparent death. Life, then, is merely interrupted at some point and later resumed upon re-establishment of the excluded necessities of life. In this respect the actively living plant resembles a working clock, the plant in a state of apparent death simulating a time-piece which is wound up but temporarily arrested from functioning.

In plants which fruit only once the ultimate age is closely correlated with time of flowering. Under normal conditions such a plant postpones flower and fruit formation until such time as it can produce or has stored up through the activity of its leaves a sufficient supply of formative materials. After fruiting it declines as the result of the consumption of this reserve material.

But when we hinder flower formation by whatsoever means, whether it be through insufficient light, certain temperatures or through greater humidity of the soil and air, we guard the plant against death and defer the latter. But just as soon as it has flowered and fruited, the organic reserves are completely emptied and utilized and a yellowing of the leaves or of the entire plant accompanies this process; at the same time, the chloroplasts are destroyed and their proteins move into the seeds. Deprived then of its chloroplasts the chlorotic leaf can no longer function normally or serve as an organ of nutrition and for this reason the plant dies after ripening of its seeds.

The fact that an organ dies when it has once become functionless can be observed all along the way. A petiole robbed of its blade, a pedicel separated from its flowers, dies or falls off; a tendril, so

unfortunate as not to find any support, becomes stunted, and leaves which are not exposed to light and developed in their natural way, die. In other words, organs which can not pursue their natural destinies die early. But when their functioning period is prolonged by artificial means beyond the normal, life is extended, to which fact de Vries called attention. So it is with the pedicel and petiole of *Pelargonium*, *Begonia* and *Torenia* which have been transformed into a part of the branching system: it is true also of budless rooted leaves and of the gall-bearing male flower axes of nettle, hops and maize. And when grafting of a perennial plant upon an annual (*Abutilon* on *Modiola*) gives the annual a perennial nature, we also have a functioning period which is induced in an annual stem. The *Abutilon* scion draws water together with dissolved mineral salts through the stem of the annual and compels it to function longer than it ordinarily would. Associated with this intensification and extension of function is a richer provision of nutrients. The same effect is secured in the branching system above a girdle wound and as a result of the subsequent accumulation of valuable formative materials, premature dropping of the fruit is prevented.

Inadequate nutrition, on the other hand, shortens life, for starving leaves soon turn yellow and suffer premature death.

Though much experience lies behind us we are still only beginning to learn how to prolong the life of plants. The more science advances the more do we learn to control plants by experiments and to come to the well founded view that the macrobiotics of plants will also make advances, but only to a certain degree, for in the last analysis death destroys every form of life, except the unicellular organisms, whether it be a flower of a day, an annual herb or a thousand-year old giant tree.

CHAPTER V

REJUVENESCENCE

There are frequently associated with the life extension of plants phenomena which we are accustomed to designate as constituting rejuvenescence, and which, therefore, must be briefly touched upon.

The word rejuvenescence is employed in connection with various phenomena of plant life. We speak, for instance, of cell rejuvenescence when, as in the case of certain algae, *e.g.*, *Oedogonium*, *Vaucheria* and others, the old cell membrane bursts and the old protoplast rounds off and escapes as a naked swarm spore to swim about for a while, finally coming to rest and surrounding itself with a new cell wall, only to germinate again into a new cellular filament. The protoplasts of developing moss and fern spores as well as pollen cells of flowering plants surround themselves with their own cell membranes while still within their encompassing mother-cells and in this way become self-sustaining while the old cell membranes disappear. In such cases, too, we speak of cell rejuvenescence.

The word is likewise familiar to the gardener.²⁷⁶ If a tree, for instance, begins to age and its growth becomes sluggish, this condition can be remedied for a while by cutting back the branches and twigs one- to two-thirds their length. Dormant buds are thereby awakened which then develop strong and rapidly growing shoots, thus contributing toward a new development of the crown, toward a rejuvenescence.

Various plants produce strongly geotropic shoots of an unusually marked erect growth in addition to the average or weak ones. These vigorous shoots withdraw the stream of nutrients from the weaker neighboring shoots and appropriate it to themselves. By removal in fruit-tree culture of these energetically developing shoots, known to the practical man as suckers, rejuvenescence of the crown is encouraged. I have noted elsewhere²⁷⁷ that many trees can endure a severe annual or even more frequent cutting-back to the base of the main branches (*Aesculus*, *Robinia*,) while others (*Salix*) can undergo formal trimming. They all respond to this peremptory treatment by producing strong erect shoots which develop before long into a new, stately and rejuvenated crown. This rapid re-establishment of a branching system is to be accounted for by the

large supply of reserve materials in the form of starch, fats and proteins which are stored in the stem and suddenly placed at the disposal of the young twigs.

If we consider, further, the healing of wounds we are again confronted with rejuvenescence of the cell. As an example, we may place the two halves of a severed potato tuber in a damp compartment, preferably under a bell glass. The parenchyma cells, rich in starch, which lie directly beneath the cut cells of the wound surface, are mature cells and would so remain throughout their lives under normal conditions. Stimulated by the wounding to divide they gradually form a meristem, however, and from this a periderm layer which very effectively cuts off the wounded surface. The permanent cells are thus caused by the injury to revert to an earlier stage of development; to some degree, to an embryonic condition, and they then become what they once were, meristematic cells; in other words, they become rejuvenated. This illustrates especially well just what is meant by rejuvenescence, namely, a reversion from an older to an earlier stage.

Alexander Braun²⁷⁸ had a similar but broader conception when he characterized rejuvenescence as "the surrender of an already acquired state and the return to a new beginning." In his work devoted to the subject Braun gives a great series of pertinent observations and so long as he deals with these and other facts one can readily follow him. When he indulges in the natural philosophy of his time,²⁷⁹ however, it is not so easy.

Several workers^{280, 281, 282} have been occupied with the microscopic changes which potato cells exhibit during rejuvenescence and the associated healing of a wound. To begin with, the cells which are about to undergo rejuvenescence are freed of starch, and wax larger and richer in protein; the nuclei become richer in chromatic material, increase in size, and divide. Hand in hand with the latter process is division of the cells themselves, giving rise to the formation of a phellogen and finally of a periderm which seals the wound very effectively and guards it against water-loss and attack by fungi.

Haberlandt²⁸³ established the interesting fact that if decomposition products of mechanically killed or injured cells remain upon a wounded surface, such accumulation provokes cell divisions and thus makes healing of the wound possible. The following experiment

from Haberlandt's treatise may be cited to secure a better understanding of this process. A disc, one to two centimeters thick, is cut from a kohlrabi (*Brassica oleracea gongylodes*) and divided into four sectors. One of the sectors is not rinsed, the second is washed for five to twenty minutes under a strong stream of water, the third is rinsed and covered with a thin layer of kohlrabi mash, secured by

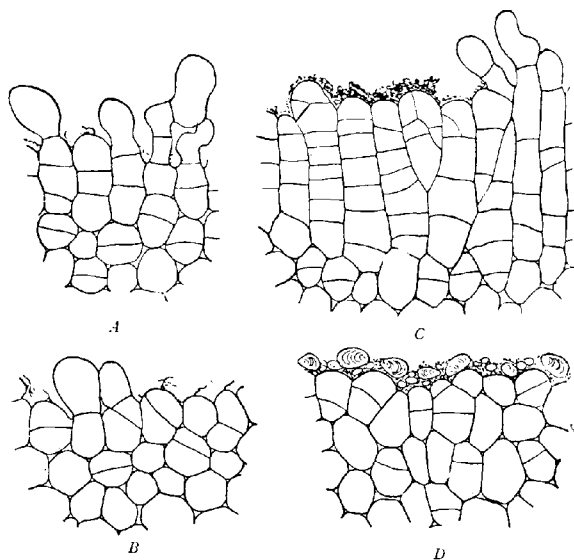


FIG. 23. Cell divisions, induced by wound hormones, beneath the wound surface of 4 sectors from a disc of kohlrabi. A: wounded surface not rinsed; B: wounded surface rinsed with water; C: wounded surface rinsed and covered with kohlrabi mash; D: wounded surface rinsed and covered with potato mash. From Haberlandt.

crushing small pieces, and the fourth is rinsed off and covered with a thin layer of potato mash. In figure 23 we see the results:

A shows some callus cells with several underlying cell divisions induced by the wound hormone left lying on the cut surface.

B shows fewer callus cells and cell divisions because the wound hormones were removed by rinsing.

C shows only a few callus cells but unusually many cell divisions, especially beneath the kohlrabi mash.

D shows divisions as in B, every cell having divided at least once.

Haberlandt concluded from this and similar experiments that the decomposition products of the killed cells function as division hormones. The occurrence of some divisions in the rinsed sector B is attributable to the fact that it is impossible to remove every bit of protoplasm which has been killed, and if divisions in sector D under potato mash do not take place more frequently than in the rinsed sector B, it is because of the specificity of the wound hormone. It is apparent from further investigations of Haberlandt not only that substances effective on wounds develop in the killed cells, but that wound hormones can arise in injured but still living cells (hairs, epidermal cells, guard cells), inducing typical nuclear and cell divisions.

Wehnelt²²⁴ has of late attempted to arrive at a better understanding of the wound hormone discovered by Haberlandt. The young pericarp of *Phaseolus* has been shown to be an excellent subject in this work. On its inner surface it possesses a comparatively abundant mass of tissue free of vascular bundles and consisting of uniformly similar cells. By cutting the pericarp along the ventral suture this tissue is laid free, and tissue sap, extracts or other organic and inorganic substances may be placed upon the center of the concave inner side. The untreated neighboring tissue serves as a control. By this technique, and in contrast with previous investigations, the influence of a wound upon the region under investigation is completely excluded. If tissue sap of young bean leaves is placed on the pericarp cells, the cells directly beneath this covering grow upward by means of numerous divisions and produce considerable wound tissue; the untreated area remains unchanged, on the other hand. The juice of tissues strained through ultra-fine filters also induces the formation of wound tissues. Fresh juice remained thermostable, even with heating under pressure and higher temperature. Experiments were also carried out with a variety of organic material, and these, too, such as white of egg, horse serum, haemoglobin, deuto-albumin, various insulin preparations and agar-agar, had the same intensive effect on the cells of the pericarp as did the tissue sap itself. Of the mineral substances that were tried, pure water induced growth but not cell

division. Cane sugar and Knop's nutrient solution also failed to induce division.

In his work the author avoids applying the expression hormone to the effective substances because the thought can not be disregarded, "that it does not involve a hormonal, *i.e.*, a physiological, specific effect of one or more bodies, possibly proteolytic products or lipoids, but rather a non-specific increase of cellular activity, expressed in a return to a meristematic condition." The assumption that a hormonal effect is involved is refuted by the fact that the same effect is produced by such different substances as tissue sap, serum, albumin and agar.

Rejuvenescence is experienced also by many cells when they form a callus, a term which is understood to include the formation of all parenchyma tissue formed by the plant on a wounded surface after injury, and appearing, particularly, on incisions, frost cracks, girdlings and at the base of cuttings. All tissue layers may participate in this callus formation, first the cambium and then the parenchyma of the pith and cortex. In the latter case we speak of a rejuvenation, but not with respect to the cambial cells, for they are always in an embryonic state.

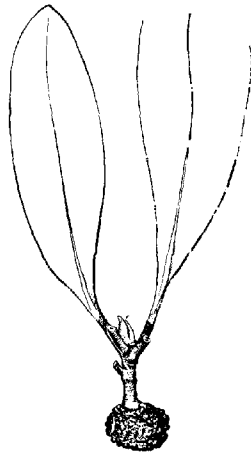


FIG. 24. *Rhododendron arboreum*. A cutting with callus. Original.

Whenever a tissue is injured and the adjacent uninjured cells replace the wounded ones by growth or cell division, then we speak of regeneration, and for this reason we can designate the wound-healing of the potato and callus formation as regeneration. If the regeneration proceeds so far that the consequences of wounding are fully removed and the former state of the wounded organ is fully re-established in every respect, we have restitution. Detailed and numerous examples of this can be found in the works of Küster²⁵⁵ and Korschelt.²⁵⁶ Here, however, we may only say that regeneration as well as restitution frequently are associated with rejuvenescence and that the two usually go hand in hand.

Another example of rejuvenescence of cells is furnished by the galls which so often develop on plants.²⁵⁷ Whether these be in-

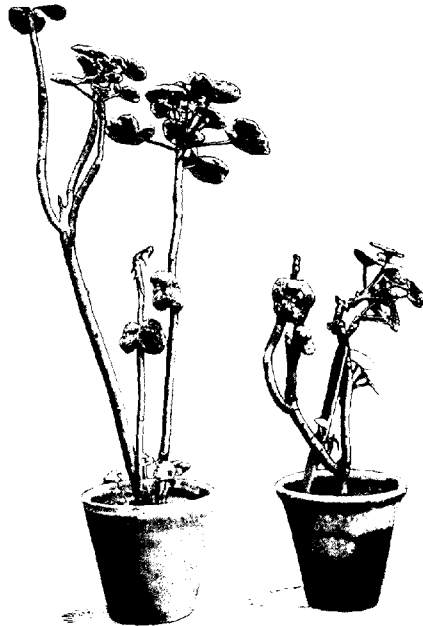


FIG. 25. *Pelargonium zonale*. Crown-galls on the stems. Original.

duced by fungal growth or by the puncture and egg-laying of an insect or other animal, the permanent cells of the host in all cases are induced to undergo division by virtue of the stimulus, and formation of the gall is thereby brought about.

So-called crown-galls, intensively investigated particularly by Smith,^{285a, b} also furnish an example of rejuvenated cells. Smith made the significant discovery that the tumors arising on various woody perennials and on woody and herbaceous annuals are caused by a specific agent, the bacterium *Bacillus tumefaciens*. Any cambial cell as well as any parenchyma cell, whether it be in the cortex, pith or ray, can divide under the influence of this bacterium and by continued divisions can become the initial point of a tumor.

CHAPTER VI

APPARENT DEATH

Among plants there are some which continue to grow uninterruptedly; others, after a certain period of active growth, rest for a while and later resume growth in order to prolong their lives, eventually entering another more or less protracted period of rest. We observe a striking example of this rhythm in many trees and shrubs which in spring awaken from their winter rest, produce shoots, acquire foliage, flower and fruit, and in autumn discard their leaves and enter upon another period of rest. The following spring the same sequence is again repeated. In speaking of this dormancy of a tree, of a potato tuber or of a bulb, we do not imply, however, that the life phenomena within these organs come to a complete standstill; this certainly is not the case, for the tree respire also in winter, the sap moves and metabolic processes take place.

The intensity of the life phenomena under these circumstances, to be sure, is very unlike among different resting plants and their organs. In a tree or a potato tuber stored in the cellar they are relatively intense, considerably less so in a seed resting in damp earth, and almost completely at a standstill in a dried seed. In the latter case it is difficult to determine, unless one makes a germination test, whether the seed is only dormant or actually dead. Though still viable, it gives the appearance of being dead, but actually is only in a state of apparent death. This apparent death presents an interesting phenomenon which is within the compass of this book, and for this reason we shall concern ourselves somewhat with it.

THE CONCEPT OF APPARENT DEATH

The idea is prevalent in the mind of the layman that in every single case it can be easily and quickly determined whether a plant or animal is dead or alive. It is also commonly believed that it is readily possible to ascertain the exact time at which death sets in. When a renowned person, an emperor or a king, perishes, the exact ~~minute~~ minute of his death is customarily recorded, and this provokes in the mind of the laity the impression that death occurs instantly and that between life and death there is a sharp distinction.

A man is usually pronounced as being dead when respiration has permanently ceased. In such cases, the physician substantiates and vouches for the cessation of life. This, however, is only by conventional agreement, for actually there can still be much life in the "dead" man. If a man be decapitated or hanged the physician pronounces him dead after the execution, but if the "dead" man be dissected a few minutes after the official pronouncement of death, the muscles contract upon being cut, and the entrails become agitated by lively peristaltic movement. Upon opening of the pericardium and the consequential contact with oxygen of the air, the heart begins to pulsate for several minutes, even for a quarter of an hour, and if it comes to a standstill, a needle-prick suffices to produce one or more pulsations, and two to four hours after "death" stimulation of the nerves causes a jerking of muscles.

Kuliabko²⁸⁹ has gone so far as to secure pulsations of the ventricles and auricles in the hearts of deceased children, up to 30 hours after "death," by flushing them with a certain solution. The epithelium covering the inner surface of air passages, of the larynx, of the trachea and of the bronchia, exhibits a pronounced rhythmic pulsation in the corpse for days after the heart has ceased. Pütter²⁹⁰ records in an interesting article that epithelial movement could be observed (Busse) in the mucous membrane of a nasal polyp which had been operated upon, when it was kept at 4° to 5° C. for 12, 14, and in one case for 18 days after the operation.

The colorless blood corpuscles and spermatozooids of man, too, can long outlive the individual,^{291a-c} and other analogies are offered by plants. As a rule, dahlias freeze upon the advent of the first severe frost of autumn. According as the sun strikes the frozen leaves, they thaw out, turn black and hang limp from the twigs. Everyone at such times regards the leaf as dead because of its appearance. When I examined such frozen leaves under the microscope some years ago,²⁹² I found almost all the cells dead, to be sure, but the majority of guard cells belonging to the numerous stomata on the lower surface were alive. The guard cells are much more resistant against cold and other injurious factors than are the other cells of the leaf. If we then regard such a frozen leaf as dead, we are but partly correct; properly speaking, we can only say that such a leaf is no longer alive as a whole but is for the most part dead.

Death, then, does not necessarily overtake an organism completely and instantaneously but proceeds in its course gradually.

Just as difficulties are presented in stating a precise moment when death overtakes a higher organism, it is likewise not a simple matter in many cases to determine, merely by inspection and without more exact examination, whether an organism, a tissue or a cell is dead or alive. An air-dry kernel of corn, lying on a table, displays no indications of life whatsoever. It neither grows, assimilates nor moves; in short, it betrays no sign of being alive. Only when it germinates and forms root, stem and leaf, upon provision of moist earth and other favorable growth conditions, is one in a position to say that the kernel was not dead but alive. In a dry condition, however, so far as the eye can judge, it is no different from a dead grain. Any organism, whether it be plant or animal, which displays no noticeable signs of life but which, nevertheless, is alive, we say is apparently dead. The kernel of corn which still harbors the ability to germinate, though it shows no indications of life, is apparently dead. Only when it completely loses vitality is it dead. Natural death is the permanent standstill of life or, in other words, the final interruption of metabolism in the sense of assimilation and dissimulation.

LIFE-REACTIONS

It appears to be of considerable importance in many cases for the physiologist to know whether a cell is dead or alive. Decision in this direction presents no difficulty in many cases as, for example, when one observes protoplasmic streaming or nuclear division take place within the cell. Such conspicuous indications of life can be established only in the rarest cases, however, and for this reason we depend upon a variety of methods, so-called life-reactions, which very often make it possible to distinguish in doubtful cases between the living and the dead. Four of these methods will be discussed here:

(1) One of the best means of becoming convinced that a plant cell is alive is offered by plasmolysis. If a living cell, for example, an epidermal cell from a leaf of *Tradescantia* or from a moss, is placed in a 10% solution of kitchen salt, water will be withdrawn from the cell, the protoplasm will recede from the cell wall, shrink together and round up. This withdrawal of plasma from the wall as the result of a water-removing technique, is known as plasmolysis.

A cell in which plasmolysis can be demonstrated is regarded as being alive, for dead cells do not show this feature. Though this life-reaction is of excellent service, it not infrequently happens that such shrinkage can not properly take place, either because the cell is too small or because its cavity is narrow or clogged with reserve materials.

(2) Electrical induction shocks can also be employed to indicate the presence of life. Upon such tests the living protoplasm suddenly draws together or its organization is disrupted. As contrasted with plasmolysis, this method yields much less satisfactory results because in many cases it is ineffective.

(3) Loew²⁹³ and Bokorny have recommended the silver reaction. They found that living cells reduce silver within their interiors from very dilute and weakly alkaline silver solutions. If living cells of *Spirogyra*, *Zygnema*, or of other plants are placed in a dilute alkaline silver solution for six to twelve hours, the protoplasm darkens as a result of silver reduction which takes place. Dead cells do not give this reaction and for this reason the two investigators recognize in the method a useful life-reaction. As these two workers themselves found, this reaction unfortunately does not take place in all living cells, and its use, therefore, is limited.

I have been able to show that living chloroplasts, when treated with a silver salt, for example, with an aqueous solution of silver sulfate, darken rapidly and intensively, while dead plastids do not do so. This is a striking indication of how the chemical nature of a living part of the cell can change immediately upon the appearance of death.^{294a, b}

(4) Living protoplasm possesses the quality of being impermeable toward certain pigments, for example, the blue, violet or red coloring matter of many leaves, caused by the anthocyanin which is so widely distributed in the plant kingdom. Dead protoplasm, on the other hand, not only is permeable to this pigment but also accumulates it. One can easily be convinced of this by cutting from a living red beet two equal cubes and placing them in water, the one immediately after being cut, the other after first being killed in an air bath of 60° C. In the first case, that of the living beet, the coloring matter does not come out and the water remains wholly colorless, while in the second, the killed beet, the color comes out of the tissue abundantly and stains the water deep red.

The nature of protoplasm to be impervious in a living condition to certain substances can also be employed as a life-reaction.

If none of these methods suffices alone, we must resort to a combination of them in order to arrive at a halfway certain determination.

The most certain test of life rests, after all, in the establishment of further development. If a cell, a tissue or an embryo displays such development, there can be no doubt of its being alive.

THE OCCURRENCE OF APPARENT DEATH

The bear-animalcule (Fig. 26), *Macrobiotus Hufelandii*, furnishes one of the best known examples of apparent death. This

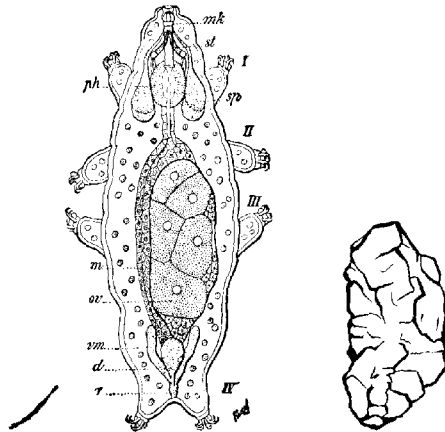


FIG. 26. *Macrobiotus Hufelandii*, a bear-animalcule. On left: actively alive; on right: in apparent death, dried out. From Hertwig and Verworn, respectively.

mite-like animal, belonging to the Tardigrada, usually lives in mossy swards, and since the latter are frequently found on shingle roofs, the animalcules get into the gutters where they survive and can readily be found in the dried-out dirt. In Nature they are exposed to desiccation at which times their movements slow down more and more until finally they shrink into insignificant little clumps, no longer displaying any indications of life. In this

state of apparent death the little animal can long persist but when again in a position to take up water after a rain it begins to enlarge and resumes its usual activity.

Similar to this is the behavior of paste eels, belonging to the nematodes, which thrive in sick kernels of wheat, as well as of many infusoria, flagellates and numerous wheel animalcules.²⁹⁵ An especially interesting case among the latter is that of *Callidina*, which lives in the foliar tracheids of a liverwort, *Frullania dilatata*, frequently found on tree trunks. The animalcules, *Callidina symbiotica* and *C. Leitgebii*, dwell preferably in the swollen tracheids, probably because they there find favorable nutritive conditions. When the liverwort dries, the little animals enter a state of apparent death. But just as soon as the hepatic is moistened by rain-water the shriveled animalcules acquire new life and their rotiform organs become active. These wheel animalcules can be brought back to activity from a latent existence also by dampening them with a drop of water after they have lain in the herbarium with the liverwort for years.

Plant life, too, offers abundant examples of apparent death²⁹⁶ among which only some of the most important and most interesting will be described or mentioned.

Liverworts. Many liverworts which are frequently subjected to desiccation in Nature long retain life in a dried condition. Schröder noticed that *Corsinia marchantioides* resumed growth when subjected to normal conditions after having been in the herbarium for seven months.

Mosses. The ability to withstand desiccation appears to be developed to a much greater degree in mosses than in liverworts. It is particularly evident in those which live in the wild on dry locations and which have consequently adapted themselves to an alternation of wetting and drying. Such mosses are extraordinarily retentive of life. *Barbula unguiculata* has already undergone atmospheric drying-out on a piece of tufa for a period of 20 weeks and was then subjected to additional desiccation through the agency of sulphuric acid, after which treatment every cell proved to be alive when moistened, and the plant resumed growth.

We can say, in general and according to Schröder, that, except for their spores, species which are accustomed to drying-out also die after a few years, five at the outside. Their spores can endure

much longer, however, in a state of apparent death. Schimper found that moss spores which had lain in the herbarium for 50 years germinated as if they had been taken from fresh plants.

Algae. While many algae can not endure drying-out at all, others are distinguished by their ability to do so. The latter are found particularly in the family *Palmellaceae*. *Pleurococcus vulgaris*, which forms the green masses on the northwest side of many tree trunks, has exhibited life after 20 long weeks of severe desiccation.

Fungi. Many bacteria do not withstand drying; others, to the contrary, do. Certain soil bacteria can endure in a dry condition for surprisingly long periods and then they acquire renewed life.

Nestler,²⁶⁷ who removed bacteria from the soil adhering to specimens in a very old moss herbarium, and then investigated their viability, came to the interesting conclusion "that some spore-forming bacteria—*Bacillus vulgaris*, *B. mycoides*, *B. subtilis*—can endure desiccation at ordinary temperatures for a decade and can retain life for at least 92 years."

It is not often that the vegetative bodies of higher fungi withstand drying-out, while, on the other hand, there are many spores which possess this adaptation to a marked degree. Brefeld obtained new plants upon the germination of six-year old spores of the mold *Aspergillus flavus*.

Liebenberg studied smut spores which had been preserved for varying lengths of time in the herbarium. "The ability to germinate was retained in the spores of *Tilletia caries* after 8½ years, of *Ustilago carbo* after 7½ years, of *U. Kolaczki*, *U. Crameri* and *U. destruens* after 5½ years, and of *U. Tulasnei* after 6½ years. There appears to be no doubt that these periods could be extended still more without significant injury to the germinating ability of these spores."²⁶⁸

Seeds. Just as the capacity to withstand drying out to an air-dry condition without loss of viability is found among flowerless plants particularly in their spores, so among flowering plants this feature is eminently developed only in the seeds. The behavior of the latter, however, is very variable in this respect.

According to investigations by Hildebrand, the seeds of *Oxalis rubella* and *O. lanceacfolia* and their relatives germinate immediately after opening of the fruit and are killed by drying out. In

willow seeds the ability to germinate is retained for only a few days or weeks. Nakajima²⁹⁹ was able to show that the germinating capacity of the seeds of various species, *Salix opaca*, *S. japonica* and *S. Reinii*, was considerably longer than normal if the seeds were kept at ordinary dryness and a temperature of 12° or 13° C. Under these conditions 60% of the seeds were still viable after 150 days and a few germinated after even 320 days. Aside from these and a few other cases, most seeds retain their germinability for years.

We are indebted to Burgerstein³⁰⁰ for investigations in this direction with respect to grains. We learn from them that 70% to 90% germination was secured in barley, wheat and oats after the seeds had been kept for 10 years wrapped in paper in a drawer, while rye lost its viability during the same period. Other seeds remain viable for still greater periods.

The extensive investigations of Becquerel and Ewart furnish additional information concerning maximum periods of viability. Becquerel³⁰¹ procured the oldest seeds which he could obtain and whose ages were definitely known from seed collections and herbaria. Altogether he studied 500 species belonging to 30 families, and the periods of viability ranged from 25 to 135 years. They were all subjected to conditions favorable for germination but only four families gave positive results, Compositae, Nclumbiaceae, Malvaceae and Labiatae. Of the Leguminosae the following species showed the indicated germination of their seeds:

| | | |
|-------------------------------------|-------------|--------------|
| <i>Cassia bicaupularis</i> | 3 out of 10 | 87 years old |
| <i>Cytisus biflorus</i> | 2 " " 10 | 84 " " |
| <i>Leucaena leucocephala</i> | 2 " " 10 | 72 " " |
| <i>Trifolium arvense</i> | 2 " " 10 | 68 " " |
| <i>Ervum Lens</i> | 1 " " 10 | 65 " " |
| <i>Dioecia pauciflora</i> | 4 " " 10 | 65 " " |
| <i>Cytisus austriacus</i> | 1 " " 10 | 63 " " |
| <i>Melilotus luteus</i> | 3 " " 10 | 55 " " |
| <i>Acacia distachya</i> | 5 " " 10 | 53 " " |
| <i>Mimosa glomerata</i> | 5 " " 10 | 53 " " |
| <i>Crotolaria ramosissima</i> | 1 " " 10 | 39 " " |
| <i>Nomismia munimularia</i> | 2 " " 10 | 38 " " |
| <i>Astragalus brachyceras</i> | 2 " " 10 | 38 " " |
| <i>Dolichos funarius</i> | 2 " " 10 | 37 " " |
| <i>Acacia cornigera</i> | 5 " " 10 | 37 " " |
| <i>Trifolium caespitosum</i> | 2 " " 10 | 28 " " |

In the Nelumbiaceae the seeds of three species germinated:

| | | |
|------------------------------------|------------|--------------|
| <i>Nelumbium codophyllum</i> | 4 out of 5 | 56 years old |
| " <i>asperifolium</i> | 4 " " 5 | 48 " " |
| " <i>speciosum</i> | 9 " " 10 | 18 " " |

Among 15 species of the Malvaceae only the following germinated:

| | | |
|------------------------------------|-------------|--------------|
| <i>Lavatera Pseudo-olbia</i> | 2 out of 10 | 64 years old |
|------------------------------------|-------------|--------------|

Among 14 species of the Labiatae only the following germinated:

| | | |
|-----------------------------------|-------------|--------------|
| <i>Stachys nepetaefolia</i> | 1 out of 10 | 77 years old |
|-----------------------------------|-------------|--------------|

The interesting fact is apparent from these comprehensive investigations of Becquerel that there are seeds, those of *Cassia bicapsularis*, which can retain their ability to germinate for 87 years.

The very long-lived seeds, those of 50 to 80 years tenure, are always provided with a thick shell, impervious to water and air.

From the observations of Ewart³⁰² these periods of longevity have been surpassed by the seeds of *Howea heterophylla*. Of twelve seeds of this palm which were 105 years old, two germinated. Upon investigating 2500 species Ewart became convinced that the longest possible period of germinating ability might be between 150 and 250 years in the Leguminosae. In the Malvaceae it lies between 50 and 150 years. Ewart's experiments were carried out primarily with seeds which had been kept in dry air for years and he believes that impervious seeds would remain alive still longer if they lay in the ground.

Especially interesting are the observations of Ohga³⁰³ on the germinating power of seeds of *Nelumbo nucifera*, the Indian lotus, which were found buried in peat in Manchuria. Near the northern end of Kwangtung province in southern Manchuria is the village of Pulante and not far from there the village of Liu-chia-tung. The plain to the north of the latter is the site where seeds of *Nelumbo* are buried at a depth of one-half to two-thirds of a meter in a layer of peat one-third to one-half meter thick. For various reasons the author believed that the seeds had lain in the peat for at least 120 years and were perhaps 200 to 400 years old. The peasants use the burned peat for fuel and the children eat the seeds. In spite of this great age the embryos were still green and the endosperm yellowish white. When the seeds were placed in water after being exhumed and left there for eight months at a temperature of

15° to 20° C., there was no noticeable change, for no water could penetrate through the exceedingly tough seed coat. If the seeds were filed at one or both ends, however, they took up water, swelled and germinated without exception, in some cases after four days.

Further investigations of Ohga³⁰⁴ showed that these lotus fruits in all probability are over 160 or 250 years old. Despite this advanced age, they germinated 100%. If seeds of *Nelumbo* can remain alive in peat for so long, it is very likely that the peat has some preserving influence on them. Investigations on this point would be worthwhile to determine whether or not this life-preserving effect of peat is not of some effect on the seeds and organs of other plants.

It is still reported in the literature at times that wheat seeds several thousand years old from mummy graves of ancient Egypt are still viable. Such reports are without factual foundation, however, and have long been disproved through various observations. On May 10, 1847, Münter³⁰⁵ reported that wheat and six-rowed barley from Egyptian mummies had completely lost their germinability. Unger³⁰⁶ writes, concerning mummy wheat: "I brought a considerable quantity in a well sealed clay vessel from Thebes back to Europe. Director Schott was kind enough to plant what appeared to be the best and fullest grains but they failed to germinate, regardless of the care given them." He says elsewhere:³⁰⁷ "I want to add, furthermore, that I have again tested the germinating ability of some grains from the graves of mummies as I did once before, this time using those which appeared to me to be the best preserved. I examined seeds of wheat as well as of *Phalaris paradoxa*. The result was the same, namely, that even under the most favorable conditions decay rather than development set in." Attention may be directed finally to the work of Wittmack, concerning which he remarks: "The experiments which I pursued with mummy wheat, found in a sarcophagus of the Grecian epoch in old Memphis and secured as genuine by the agricultural museum from Dr. Figar Bey, Egyptian commissioner, for the Paris exposition of 1867, proved wholly unsuccessful in spite of all precautions under the most varied modifications. The originally brown seeds with a mummy-like odor finally crumbled like clay in the water and the mummy-seeds of barley behaved likewise."³⁰⁸

The foregoing experiments have completely discredited the old but frequently repeated legend of the germination of mummy wheat

from ancient Egypt. Whenever experiments of this sort show positive results it is because fresh wheat has been substituted for genuinely old grains, being offered at a good price by swindlers to the tourist.

It has often been noted that on any particular spot the composition of the plant cover varies with sudden change in the soil surface. If a woods, a field or a meadow is deeply cultivated there often appear plants which previously were not at all present or only sparsely so. Where do they come from? One might suppose that seeds had been brought in by wind, water, animals or by man, or that the seeds had lain in the ground and were suddenly brought under favorable germinating conditions by the turning over of the soil. It has been shown by special investigations of Peter³⁰⁹ that the last is the case. With special care he removed plant-less areas of soil, 30 cm. on a side and 8 cm. deep, from within a woods, and then a second and a third section, and observed them in the conservatory to determine which plants, if any, appeared on the three samples. All three contained concealed living plant embryos, which in many cases developed to the seed-production stage when the soil was broken up, moistened and illuminated. Soil tests from woods which had always been woods produced only woodland plants, strawberries, raspberries, nightshade, *etc.*; apart from some isolated woodland plants, tests of planted areas on former fields or meadows showed primarily field and meadow plants, shepherd's purse, charlock, wild mustard, St. John's-wort, plantain, *etc.* Such results were secured with soil from woods which were covered by plants and whose forest cover had appeared 20 to 40 years previously. Peter concluded, therefore, that the still viable seeds had rested in the soil and remained alive for this length of time. He makes no comment as to the cause of this lengthy apparent death in the ground but it appears to be possible that the soil had a preserving effect on the seeds. This question would merit a special investigation.

It is certainly not to be expected that the germinating capacity of seeds of any one species would be the same under all circumstances, for the viability depends to a marked degree upon the way in which the seeds are preserved. If, for instance, we compare the duration of germinating ability which Burgerstein³¹⁰ found for Indian corn in Vienna with that noted by Kondo³¹¹ in Japan, there is no agreement. According to Burgerstein, Carruthers³¹² and

Dorph-Petersen,³¹³ the viability of barley seeds is, respectively, more than 15, 9 and 5 years, but only 2 years according to Kondo. Furthermore, and according to Carruthers, the viability of rape, turnip and carrot is 10, 12 and 9 years, respectively, and of rape and turnip, carrot, peas, radish and cabbage, according to Dorph-Petersen, 13, 8, 10, 11 and 9 to 10 years, but according to Kondo the figures for carrot, peas, radish and *Brassica chinensis* are 2, 4, 5 and 6 years. Kondo attributed these differences to the very moist and warm summer climate of Japan, correctly so, in my opinion, for it is well known that many seeds retain their viability longer than in ordinary moist air³¹⁴ if they are kept dry, for instance, over sulphuric acid, caustic lime, potassium chloride or other drying media.

TEMPORARY COMPLETE INTERRUPTION OF LIFE

The apparent death of seeds, spores, bacteria and of other unicellular organisms is usually brought about through desiccation, but life phenomena can be interrupted also by other factors, as low temperature. Many plants can freeze hard as a bone and others, our high alpine forms or the conifers of Siberia, for instance, survive in a completely frozen state for months at a time without suffering loss of vitality. As soon as the temperature rises sufficiently, symptoms of life again become apparent. Apart from the fact that in the course of freezing the chemical processes are reduced to a minimum because of low temperature, there is a significant removal of water associated with ice formation within the plant which likewise has an inhibiting effect upon life processes.³¹⁵

The question now arises whether life processes are completely interrupted during apparent death, whether the latter state is brought about by drying out or by freezing or by both, or whether there is still a trace of life, a *vita minima*. Kochs³¹⁶ raised this question and in order to settle it he undertook to prevent any respiration in dry viable seeds. He did this by drying the seeds for a long time in air-less tubes plugged with phosphorous pentoxide and then keeping them in sealed vacuum tubes which were connected with a Geissler tube, as is customarily employed in spectroscopic study of gases. Careful tests showed that after months of time not a trace of carbonic acid was liberated. When subjected to favorable conditions again, however, the seeds germinated. Kochs

concluded thereupon "that the seeds so treated were in a state of apparent death, down to their innermost parts." While he denied the existence of true apparent death in fully developed animals and plants, he conceded that it exists in spores and seeds.

The recent investigations of Becquerel³¹⁷ appear to be of particular importance in connection with our question. In order to test the retention of germinating power in mold spores, he dried the spores of *Mucor mucedo*, *M. racemosus*, *Rhizopus niger*, *Aspergillus glaucus*, and of other species, in small sterilized glass tubes in the presence of barium hydroxide for 14 days at 35° C. The tubes were thereupon vacuumized, sealed and laid aside from February 1908 until May 1909, and in February 1909 they were exposed for three weeks to the temperature of liquid air, -180° C., and then for 77 hours were exposed to liquid hydrogen at -235° C. On May 9, 1909, the spores were removed with all precautions against contamination and inoculated into sterile nutritive media. After only 16 hours all the spores of the Mucorineae germinated and within three days the others also. Similar investigations with seeds gave the same results.³¹⁸ Becquerel concluded from his experiments that the vitality of seeds and spores not only slowed down but completely ceased under the conditions which he created for them and which involved a state of desiccation, the absence of air, and an abnormally low temperature.

In view of these experiments we are compelled to admit that under artificial conditions there is almost certainly a genuine apparent death in the case of certain seeds and spores, and that life can be completely interrupted and again resumed after a lapse of time.

Should it ever be possible to bring seeds, bacteria and spores to the absolute zero, -273° C., where every molecular movement is arrested and every chemical reaction is eliminated, then and on the supposition that the seeds and spores would subsequently germinate, as seems very likely, the above conclusion will be the better confirmed.

Just as a locomotive is brought to a full stop by the mere movement of a lever and again put in motion by a reversal thereof; just as a fountain is turned on or off by the turn of a valve; or just as a candle is set afire by ignition or placed in a state of chemical rest

by extinguishing, so can the wheel of life be interrupted in certain cases for months, even years, and be set on its course again.

There are thousands of transitional stages from active life, from the highest fullness of life, to a true apparent death. The sprouting, flowering and fruiting tree appears to be in full life, but in autumn when it sheds its leaves and over-winters, destitute of foliage, it gives the impression of starkness, of apparent death. In spite of this the life-giving metabolism is not interrupted but only exceedingly diminished in activity. Only by artificial interference, such as we have already described, can metabolism be brought to a complete standstill in seeds, spores and other cells, and can life be wholly arrested as the movement of a machine through the medium of a lever.

In Nature, however, slight chemical changes take place in bacteria, spores and seeds which appear to be in a state of apparent death, and these changes accumulate with sufficient duration and lead to injurious disturbances and finally from merely an appearance of being dead to actual death. Just what the nature of these changes is can not be said at present. We can hardly be mistaken, however, if we assume that chemical processes are involved and that the proteins and ferments which play such a significant rôle during life, suffer physico-chemical changes with aging of the cell which render it impossible for them to sustain life any longer. American investigators,³¹⁹ too, have come to the conclusion through experiments with Turkish red wheat that the loss of germinating power in seeds is brought about by a slow coagulation of proteins. They have been able to show that the conformity to law and the formula which Buglia established for the relation between temperature and protein coagulation, applies also to the dependence of the duration of latent life upon temperature. If seeds are kept under certain conditions, for instance, their longevity can be predicted by this formula.

CHAPTER VII

OLD AGE, DEATH AND THE ALLEGED POTENTIAL PERPETUAL LIFE OF A TREE

OLD AGE AND DEATH

The trunks of many trees become hollow with age, the inner portions dying and decaying, and this change often proceeds so far that the bole consists only of the bark and a thin layer of living wood. Old willows, olive trees and redwoods are particularly inclined to develop this hollow structure. Beginning at a certain age growth commences to diminish, the annual increase of wood and bast becomes less, the annual shoots are shorter and the foliar network finer; twigs die off to a greater degree and it appears as though the resistance against outside influences, against animal and plant parasites, has worn out. All these symptoms point to the weakness of old age.³²⁰ A similar situation prevails among men where the weakness of age is a common matter, for with age there set in pathological-anatomical changes which are characteristic of the aged organism,³²¹ and one becomes smaller and sclerotic. Demange says:³²² "The basic element, the cell, first atrophies, and then there is a granular degeneration and finally a granular fatty degeneration. The binding tissue thickens through a kind of sclerosis and contributes to a certain degree to the suppression of the element whose support it forms." In animals the changes accompanying age manifest themselves in the cells in a shifting of the so-called nucleo-plasma relation and in the deposition of black pigment bodies, especially in the atrophied cells of heart muscles and ganglia. In plant cells, too, striking changes often accompany age through gradual disappearance of protoplasm and nucleus and in a shifting of the nucleo-plasma relation, *i.e.*, in a greater increase in the mass of protoplasm over against the nucleus. Changes are brought about also by the entrance of air into the cell, by the accumulation of and frequent filling of the cell lumen by waste materials such as tannin, phloroglucotannoids, phlobaphenes and by excessive incrustation of the membrane and contents with lime and silicic acid.

Oil drops frequently arise in the green aging mesophyll cells of the leaf just as black pigment bodies often accumulate with age in animal cells. These drops have been regarded by various investi-

gators sometimes as assimilation products, sometimes as waste materials.³²³ Some light has been shed on these conflicting views by the investigations of Meyer,³²⁴ which I have already summarized.³²² He divides the oil drops into two groups. In one group they arise within and come out of the chloroplasts (*Tropaeolum*), building the assimilation secretions. In the other they constitute the mesophyll secretion (Fig. 27), oil drops "which are found

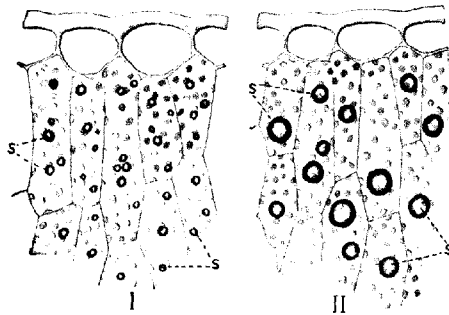


FIG. 27. Mesophyll secretion in upper surface of leaf of *Taxus baccata*. I: one-year old leaf; II: four-year old leaf. Secretion much greater in the older leaf. $\times 285$. Original.

deposited in the cytoplasm of the mesophyll cells, are wholly or to a large degree soluble in excessive alcohol and chloroform, turn brown with osmic acid, are wholly volatile or nearly so, possess no striking odor or taste, and which are less developed in the young leaves than in the older" (*Illex Aquifolium*).

The assimilation secretion represents a by-product which arises from carbonic acid assimilation. It appears in the chloroplasts first in the form of indefinite globules, but with continued assimilation they increase to such an extent that finally they are discharged from the chloroplasts in the form of drops. Hence leaves which have developed in total darkness are free of assimilation secretions. This indicates strongly that they are excretion substances.

Mesophyll secretions have been found in many species of angiosperms and gymnosperms, especially in the evergreens. Once secreted, they no longer enter into life processes but merely accumulate within the aging cells (Fig. 27).

The law of the "grand period" is in harmony with the idea that the plant ages and has its ascending and descending course of development, eventually terminating in death. According to this law, a part of a plant, such as a young cross-sectional area behind the root-tip, first elongates slowly, then progressively more rapidly until for a while it displays a maximum growth, and then progressively decreases until finally growth ceases entirely. This holds true for the most part not only for cells and organs but—and this is frequently overlooked or not sufficiently noted—also for the entire organism. It is very interesting to picture to oneself with reference to this principle the law of growth of the tree as it is confirmed, for instance, in height growth of the spruce on sites of different suitability. "As is shown in figure 28, the course of annual

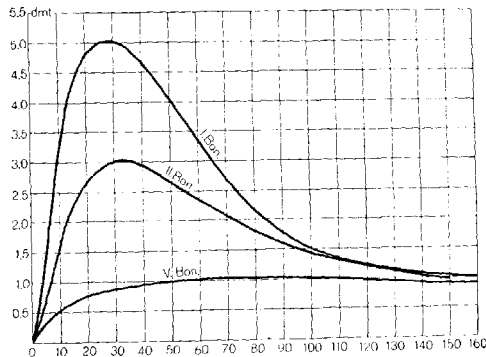


FIG. 28. Growth-curve of pine (Scots?) on three different sites. The abscissae indicate years of age, the ordinates corresponding annual increments in tenths of a meter. From v. Guttenberg.

height growth is characterized by a rapid increase from the very slow rate of its earliest youth to about half a meter on the best sites, and scarcely more than .1 m. on the poorest sites, during its 25th to 35th year; from this point it decreases rather rapidly on the best locations but only very slowly on the poorer sites, so that the annual height growth curves in advanced age on all sites approach one another to within about .1 m. The significant height difference indicated for the better and poorer sites is attributable only to

greater intensity of height growth during youth in the former whereas at an age of about 120 years it diminishes very slowly and nearly at the same rate from an annual average of 1 dm.¹³²⁵

The thickness of the annual rings, too, first shows meager development, then becomes more energetic and finally falls off, as the age of the tree increases.

As the curves in figure 28 show, decrease in the rate of growth is characteristic of old age in trees, and the same is true of animals. We are obliged to Minot¹²⁶ for detailed investigations on the daily percentage weight increases of the guinea pig for 210 days after birth, and from his data we note that this animal first grows rapidly and then progressively more and more slowly. At birth the guinea pig suffers a temporary check in its development from sudden and severe disturbance in its living conditions, but within two or three days it recovers and shows a 5% increase in weight. After 17 days it grows only 4%, after 45 days a little over 1%, and from then on the growth rate slowly diminishes and finally at the end of the first year is almost zero (Fig. 29).

If we compare the two curves in figures 28 and 29, we see that

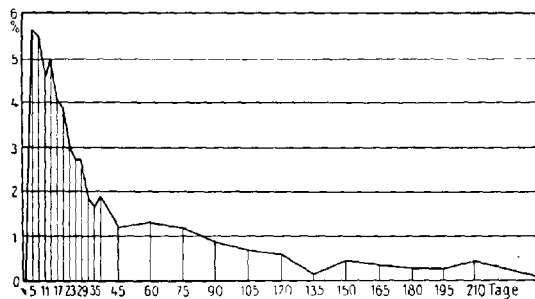


FIG. 29. Weight-curve in daily percentage increases of guinea pig. From Minot.

they both show a rapidly ascending and a rapidly descending branch which then descends further only gradually. The difference between the two curves lies primarily in the more rapid ascent and descent of the guinea pig growth curve. This is understandable since the guinea pig attains its ultimate size within one year while the tree is still growing after 100 years.

It has already been mentioned that the secretions of lower organisms exert considerable influence upon one another by a harmful sort of auto-toxication effect upon further development,³²⁷ as in infusoria, yeasts, bacteria and algae. The same situation may occur among higher plants, though I am not in agreement with Metschnikoff who claims that plants perish not by exhaustion but through poisoning as a result of their own metabolic products. In my opinion, both factors can lead to death, exhaustion as well as poisoning by certain waste materials. Autumnal leaf-fall and the scaling-off of the bark represent means by which the tree rids itself, at least partly, of such harmful or useless materials. Perhaps there is also a secretion of toxins through the root, as Molliard (1915) tried to demonstrate by experiments with peas, or through the leaves of many and especially herbaceous plants which are in a position to free themselves of certain excretions by secreting drops of water through hydathodes.³²⁸ A portion of the toxic products of metabolism remains within the tissues of the plants, however, and we need recall only the heartwood of the tree wherein, while still part of the living tree, death enters, apparently through the agency of by-products.

All this indicates that old age and finally death itself are attributable in large measure to chemical processes.

The renowned American biologist Minot³²⁹ has sought to establish an entirely different idea of senescence and natural death. He performed interesting experiments upon the growth rate of guinea pigs and found a causative relationship between the degree of cell differentiation and the rate of growth. He finds "that undifferentiated cells can divide rapidly, that those which are somewhat differentiated can divide only at a slower rate, and finally that fully differentiated cells can not divide at all. . . . Senescence is brought about by increase and differentiation of the protoplasm."³²⁹ Minot sees the justification of his idea in the fact that young cells display a reversed relationship. They possess a nucleus and a small amount of protoplasm, all of which is undifferentiated. He distinguishes two principal periods of development, the first being characterized for a much shorter period by a conspicuous increase in the nucleus; the second for a much longer period by growth and differentiation of the protoplasm. The former period is that of youth, the second, of senescence. Minot's idea, based principally upon investigations

with animal cells, is very plausible and can be applied also to plant cells because it considers old age as a phase in the ontogeny of every cell. It is regrettable that we are only slightly acquainted with the nature of protoplasmic differentiation, whether it be from the morphological, the physical or the chemical viewpoint. We see at present only that during the course of their lives the cells of multicellular organisms are adapted for certain functions, and that they become functionally differentiated and develop into a state of permanency, thereby losing their ability to divide and to become rejuvenated. Old age leads finally to death, the ultimate phase of development. We know nothing of the nature of death and a thick veil likewise envelops the essence of life, which, it is hoped, will be lifted by the future of biology.

In order to support the idea that old age and finally death are occasioned by injurious metabolic products, that is, by a kind of auto-toxication, Zlatoroff³³⁰ conducted experiments in which he cultivated chick peas in nutrient solutions to which an extract from older plants of the same kind was added. As compared with the controls lacking the extract he could detect a definite decrease of growth rate in the cultures provided with the extract. This experiment appears to me very worthy of notice, but before general conclusions can be drawn from it, investigations upon a broader basis and under more critical analysis must be made.

Weber³³¹ has provided an instructive survey upon physiological phenomena of old age in plants and I wish to call attention here to one point. Carbonic-acid assimilation takes place in the leaf, and Willstätter and Stoll³³² have shown that this process is more intense in young leaves. If we determine this intensity at different seasons of the year we find a very conspicuous decrease in this intensity during the course of the vegetative period. If we designate the quantity of CO_2 which is assimilated under optimum conditions by an amount of leaf tissue containing one gram of chlorophyll as the assimilation number, that is, "the hourly production per gram of chlorophyll," and express it by the formula

$$\frac{\text{grams of CO}_2 \text{ hourly assimilated}}{\text{grams of chlorophyll}}$$

then the assimilation number for *Sambucus nigra* is 12.2 on May 1 and only 6.2 on July 14. This decline in the assimilatory production is associated not with the time of year but with increasing age

of the leaf. In certain cases toward late autumn the power of assimilation can fall off to such a degree that it becomes nil, as in *Robinia*, *Tilia cordata* and *Ampelopsis*. "Older leaves were plucked in October and November, still in a good green condition. They displayed only very slight assimilation or nearly none at all, while younger leaves from the tips of the twigs on the same stem and at the same time still yielded good assimilation numbers. In the case of *Ampelopsis quinquefolia*, comparison of the two kinds of leaves on twigs of the same season, as well as others secured still earlier during a mild autumn, showed more than eight times as much assimilation in the younger leaves as in the older. The assimilation numbers, based upon very comparable quantities of chlorophyll content, were .9 and 7.9 for the old and young leaves, respectively.

In microscopic cross-sections of leaves which no longer are able to function, we can not perceive any changes which might be responsible for the cessation of assimilation. The chloroplasts of younger and older leaves are approximately of equal size and similarly formed. . . ." According to Willstätter and Stoll, the decrease of assimilation is controlled by an enzyme involved in the process which loses its effectiveness toward autumn.

There are also indications that respiration, of leaves, for example, slackens with age. According to Harder,³³³ this is true also of marine algae, for he says: "In nearly all plants respiration is conspicuously more intensive in younger than in older parts. This is true not only of the leaf-like portions but applies likewise to older and younger stipes of *Laminaria*."

According to Benedict,³³⁴ it is not only the old parts of the same plant which show different intensities of assimilation and dissimilation processes, but—and this is of particular interest—leaves of the same age on woody plants of different ages assimilate and respire at different intensities. Leaves of a 60-year-old vine assimilate at a lower rate than do those of a young plant raised from seeds.

Transpiration, likewise, falls off with the age of the leaf.³³⁵ Under otherwise similar conditions young leaves transpire more than do old ones. This claim, to be sure and according to Seeliger,³³⁶ must not be applied too broadly because in the yellowed leaves of poplar a change in transpiration could not be shown. Further study is necessary to determine just what changes in the leaf bring about decreased transpiration, but it is very likely that

the condition of the stomatal apparatus plays a rôle. It appears, furthermore, that the organographic character of the shoot is also involved, since in *Acer Pseudoplatanus* the leaves of root suckers transpire more actively than do those in the crown of the tree. Slogteren³³⁷ states that the stomata of younger leaves possess a greater flexibility than the older, and, according to Linsbauer,³³⁸ a rigidity usually develops in the older leaves of herbaceous plants which is recognized in a loss of stomatal regulation. "The flexibility is usually greatest at a certain intermediate age. It is especially in *Vaccinium vitis-idaea* that I have found the stomata as a rule almost entirely closed on current shoots during mid-summer, while those of the previous year's leaves react in a typical manner toward variations in light and moisture. By the infiltration method one can easily be convinced of this at any time."

Neger³³⁹ has the following to say respecting conifer needles. "If we examine the individual annual shoots of the spruce, fir, etc., with respect to their water content and transpiration, we find that the water content decreases with advancing age while transpiration is greater, the older the shoot. From this we can conclude without doubt that the stomata of one-year needles react better to dryness, that is, they are more flexible, than older needles. Reaction of the guard cells diminishes with the age of the leaf."

As I myself have found, many stomata in old leaves of *Tradescantia guianensis* become closed insofar as the mesophyll cells bordering on the stomatal cavity grow into the cavity and obstruct it.³⁴⁰ Schwendener observed the same condition in *Camellia japonica* and *Prunus Laurocerasus*.

I have been impressed time and time again by the fact that young leaves display guttation in a most significant manner while old leaves show exudation drops to a much lesser degree or not at all. So far as my extensive observations are concerned, this is of general occurrence.

The ability to react toward external stimuli, such as gravity, light, etc., likewise decreases with age, and the same is true also of regenerative capacity and the formation of new organs, e.g., roots. I shall show this later and Goebel has demonstrated it for adventive shoots of ferns. According to this investigator,³⁴¹ seedlings show themselves to be induced by a smaller stimulus than older plants, for they are able to undergo deeper changes in organization. Young

plants of *Phyllanthus*, for instance, can change their dorsiventral lateral twigs into radial structures more readily than can the older plants. As Schneider-Orelli has observed, young apple fruits can heal their wounds after injury more easily by periderm formation than can old fruits. Young rhizoids of liverworts are still capable of regeneration, according to Kreh, but old ones, for the most part, are not so. It is known, furthermore, that galls can form only in organs which are still in a state of development.

This distinction between youth and old age is displayed also in the phenomenon of polarity, and on this point we are indebted to Vöchting³⁴² for pertinent observations. If pieces of willow twigs are suspended in the dark in a moist room, polarity is expressed by the formation of shoots at the upper end and roots at the lower end. If the twigs are young the contrast between apex and base is very sharp because the shoot develops very close to the cut surface and the root does likewise. This sharp contrast in polarity is lost in old twigs, however, for the points of origin of the shoot and root recede from the ends of the twig and approach one another "to a distance from the ends which increases with the age of the twig but which does not exceed a certain limit." The rapidity and energy of formation of new organs diminish with increasing age without, however, entirely disappearing in advanced age.

It has already been noted that yellowing of leaves is a typical indication of senescence. My observations³⁴³ in this direction were subsequently confirmed point for point by Meyer,³⁴⁴ and the gradual diminution of the chromatophores and nuclei during yellowing was shown by precise measurements. According to Meyer, the proteins are gradually dissolved in aging leaves, whereupon the nucleus becomes smaller. Kiehn³⁴⁵ has shown, furthermore, a decrease of nucleolar substance with advancing age of the leaf. Young nuclei usually contain large nucleoli, old ones relatively small nucleoli.

In animal cells, likewise, Hartmann³⁴⁶ shows that decreased size of the nucleus and usually also of the nucleolus are indications of age.

Doms³⁴⁷ is of the opinion that the cause of senescence must be present even in the young organism. It might not be detected in a structural change but only in the cause of such a change, that is, in the constitution. According to Doms, changes in the nuclei as the real "bearers of form" are involved in old age.

As far as the protoplasm is concerned, Schwarz³⁴⁸ has already noted that the cytoplasm swells very markedly in very young parts of plants, that vacuoles form in older parts and that in very old portions inhibition as well as vacuole formation may not take place.

According to Chifflet, the molecular movement of Brown can be observed satisfactorily only in young protoplasm and much less so in aging plasma. Russo³⁴⁹ also finds under ultramicroscopic observation that the tiny particles in young cells are in much more active motion than in old cells, probably because viscosity of the plasma increases with age.

Old and young cells show a different reaction also toward pigments. According to Weber's work, already referred to, young cells of animal tissue, and blood possess basophilic protoplasm, allegedly conditioned by a specific substance contained in the plasma. Demole³⁵⁰ refers to an analogous behavior in plant cells. With suitable dyes the growing points of *Elodea* and *Osmunda* show a basophilic character of the plasma which disappears, however, as the cell ages.

Zacharias,³⁵¹ likewise, points out that "the aging nuclei of tracheal cells with apparently completed wall thickening are distinguishable from the younger growing nuclei by their lesser amount of material soluble in gastric juice. Digestible substances outside the nucleolus in the aging nuclei were not present in demonstrable amounts, as was the case in young nuclei."

How differently in many points young and old cells behave can be seen from the following. If we grow beans or other seedlings in calcium-free solutions, growing regions of the organs die, while fully grown parts remain alive. The stem of the scarlet runner dies from lack of calcium directly under the bud of the epicotyl and turns brown, while the cotyledons, filled with reserve materials, and the fully developed portion of the stem suffer no noticeable damage.

I have noted the same thing in intramolecular respiration of the seedling. Here, too, the growing zones die first when there is a paucity of free oxygen; in other words, young growing cells succumb to intramolecular respiration much earlier than do fully developed cells.

There is no doubt that fundamental changes in the cell sap can be associated with increasing longevity. We need recall only the

red coloring of autumn foliage which is dependent upon a surfacing of the sap in aging cells with anthocyanins. When the young cells of flower buds of *Pulmonaria* and *Myosotis* first appear red and later blue-violet in the flowers which have already opened, this change rests upon a decreased acidity in the aging cells. According to Benedict, young leaves contain more acid than old ones and, according to Pantanelli, the turgor of fungal hyphae decreases with age.

Just how these individual symptoms of senescence in cells are tied up with death, whether as causative factors or only as accompanying phenomena, we do not know. During the past decades there have been great advances in the field of physical chemistry and along with the latter in colloidal chemistry. Since most constituents of the cell and all those of the protoplasm are composed of colloids, it is not surprising that attempts have been made to attribute death of the living substance to phenomena of a colloidal-chemical nature. One of the most important components of plasm is protein and one of the latter's most characteristic features is its susceptibility to coagulation. All processes which may induce protein coagulation also kill the protoplasm. As Lepeschkin²⁵² and Bechhold²⁵³ have particularly shown, there is great resemblance between coagulation of inanimate albuminous brine and that of living matter. It is not merely by chance that for a long time already the "life-curve," "old age" and even "death" of colloids have been mentioned in colloidal chemistry. Rapidly solidified gelatine is at first easily penetrated by crystalloids, but with age it becomes less permeable, and the same situation has been assumed to apply to protoplasm because it, too, is supposed to lose in permeability in old cells (Benedict). My earlier reference to the excessive incrustation of the cell membrane with mineral substances, particularly with lime and silicic acid, as a contributing factor of senescence and death, finds support in the investigations of Herzfeld and Klinger,^{254, 255} according to whom older cell membranes, which for some time have permitted the ingress and egress of materials, gradually stop up their pores and thereby lose in permeability.

IS THE TREE POTENTIALLY ENDOWED WITH PERPETUAL LIFE?

Will a higher plant, a tree, for example, guarded from all conceivable dangers to which it is normally exposed, live on without

limit, or will it eventually die because of internal factors? If supplied with sufficient nourishment and subjected to no injuries by either animal or plant, lightning, hurricane, cold, heat or other environmental influence, will it live forever? In other words, does the tree experience physiological death? The prevailing opinion among botanists is that the tree actually is endowed with perpetual life.³⁵⁶

Every bud and each root tip ends in a growing point consisting of meristem. Its cells are engaged in active division; they become converted into permanent cells at the base of the meristematic region but at the apex are rejuvenated by continued division. In a century old fir tree the primary leader, if never injured, terminates in such an old growing point. At bud tips and root tips, *i.e.*, at many points, the tree is provided, therefore, with embryonic tissue which continually grows and is rejuvenated at the same time.

Most botanists are of the opinion that these growing points do not change nor grow old but always remain young. Herein lies a great difference between the organization of higher plants and that of higher animals. The plant, because it is equipped with growing points, is able to continue growth apparently continually, never reaching a condition where its growth appears to be completed. This is in contrast with the higher animals which are without such embryonic tissues as growing points and which, therefore, conclude their growth relatively early. This condition of completed development can endure for years, constituting even the greater part of the entire period of longevity. For this reason Küster³⁵⁷ has referred to higher plants as of "open" form and to animals as of "closed" form. It is not implied by this, however, that all organs of the plant are "open," for leaves are almost always "closed" and seeds and fruits regularly so.

Belief in the potentially perpetual life of the tree is founded upon the presumption that the growing point does not change or grow old. Is this viewpoint justified?

I might direct attention first to the fact that the growing point of the embryo is the mother of all other growing points of above-ground organs. The latter, however, are not all alike; though they develop from the growing point of the plumule they, nevertheless, produce entirely different organs, foliage and flower buds, tendrils,

thorns, etc. For this reason it is necessary for many of the daughter-growing points to undergo changes in order that they may produce other products than the original.

The interesting and in my opinion heretofore greatly underestimated observations of Benedict³⁵⁸ appear to me to be of significance in this connection. I have stated elsewhere³⁵⁹ concerning them, "By numerous observations and measurements the fact could be established that in the vine and other woody plants, foliar venation suffers a definite change with increasing age of the mother

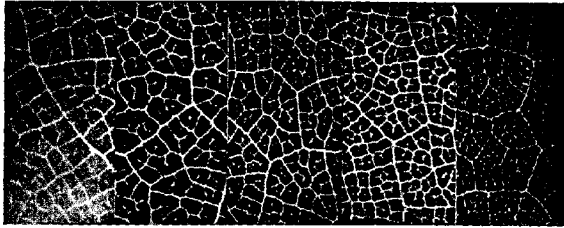


Fig. 30. *Vitis vulpina*. Venation areoles of leaves of 3-, 6-, 14-, 28- and 60-year old vein stocks. The inter-venal areas of younger leaves are larger, those of older leaves smaller. From Benedict.

stock: the areoles of the venation formed by the smallest ramifications of the system of veins become smaller (Fig. 30). In one particular case the following values were secured for *Vitis vulpina*:

| | | | | | |
|--|-------|-------|-------|-------|-------|
| No. of annual rings | 3-5 | 6-11 | 14-25 | 28-35 | 50-70 |
| Area of areole in mm. ² . . . | .4941 | .3727 | .2969 | .2211 | .1638 |

A similar condition obtains in the venous system of *Tecoma radicans*, *Salix nigra*, *Castanea dentata*, *Quercus alba* and in other trees, where old age is accompanied by a diminution of the areoles. Benedict also found, in connection with advancing age, a decrease in the intensity of carbonic acid assimilation, in respiration and in the number of stomata. Benedict rejects the assumption that the change accompanying age in foliar venation is to be attributed to lessened conduction activity of the root and stem or to an accumulation of toxins, because cuttings or shoots of old trees, though they become rooted independently and otherwise develop on their own, nevertheless, take over the diminished nature of the areoles. He concludes, therefore, that the meristem itself experiences some al-

teration with age, which leads to the weaknesses of old age or senility." The experiments of this author again furnish proof that by asexual propagation, in our case by cuttings, the peculiarities of the mother plant, such as size of venation areoles, pass unaltered to the progeny. This has long been known and much use is made of the fact in gardening practice, for it serves to perpetuate continually a newly appearing worthwhile variety, be it of growth, of shape, of color of the flower, of form or mottling of the leaf or in the quality of the fruit.

It has been found, furthermore, that it is not all the same in securing cuttings or scions from which part of the individual the cutting or scion is taken. Contrary to appearances, foliage shoots of higher plants are not all alike qualitatively but are individually different. There is shoot individuality. This is exemplified by young ivy, *Hedera Helix*, which produces either horizontal or obliquely growing plagiotropic shoots with two- to five-lobed leaves. The shoots of old stocks, on the other hand, already covered with



FIG. 31. *Hedera Helix*. Two-year old ivy plants, young form on left, tree form on right, the latter secured by means of a cutting from the flowering region. Original.

flowers, grow upright and have ovate pointed leaves. If cuttings are made from twigs in the flowering region they become rooted after a longer period of time and plants developing from them retain their upright growth and the mentioned leaf form. In this manner ivy plants are secured which the gardener knows as *Hedera*

Helix var. *arborca*, though they represent no variety but, in agreement with Goebel, a "Folgeform" of the youthful form (Figs. 31, 32).

We find also in *Ficus pumila* (*F. stipulata*) (Fig. 33) a striking distinction in size and form of leaves between younger and older plants. When I first saw this difference I could hardly believe that the foliated shoots of young and old individuals belonged to the same species.

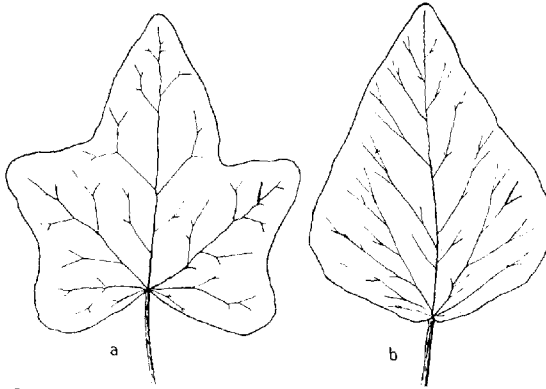


FIG. 32. *Hedera Helix*. a: leaf from a plagiotropic shoot of a young plant; b: leaf from the flowering region of an old plant. Original.

In *Broussonetia papyrifera*, too, I have noted a conspicuous difference in the leaf form of older and younger trees. The leaf of younger seedlings is three-lobed, that of an older tree entirely without lobes (Fig. 34). It is only in newly appearing shoots subsequent to injury that one may sometimes see lobed leaves make their appearance also on old trees and in like manner on root shoots.

Another very instructive case is provided by the frequently cultivated *Araucaria excelsa*, well known because of its regular and radial system of branching. The main shoot grows straight upright and from it develop verticillate horizontal lateral branches of the first order, three or four of them near the bottom, four to six or more higher up (Fig. 35). If one removes the terminal shoot of a common fir or spruce, one of the highest lateral branches of the

first rank turns upward and assumes the role of the removed main shoot. Such substitution does not take place in *Araucaria*. The lateral axis in the latter does not have the ability to become erect, but the remaining part of the main axis can produce radially arranged shoots from the leaf axils subsequent to decapitation and these shoots, used as cuttings, give normal plants with perfect radial branching. If a horizontal lateral twig of the first order is used as a cutting, however, it develops roots, to be sure, but does not yield a plant with radial branching; on the contrary, it preserves its

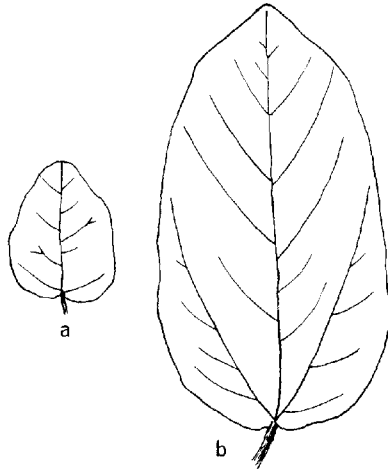


FIG. 33. *Ficus pumila* (= *F. stipulata*). a: leaf from a young plant; b: leaf from an old plant. Original.

own nature for years, most likely forever (Fig. 36). The same situation is true also of the slender lateral branches of the second order (Fig. 37).³⁶⁰ For this reason the gardener never employs lateral shoots but only the terminal shoot of the plant if he wishes to secure fine stock of radial growth.

Terminal cuttings are made also of *Agathis* (*Dammara*) because lateral shoots always remain unilateral and do not have the capacity of producing main stems.

If the yew, *Taxus baccata*, is propagated through cuttings of

lateral twigs, trees are not thereby secured but rather shrubby forms provided with twigs all the way to the ground and possessing several coordinate axes growing upright close to one another.

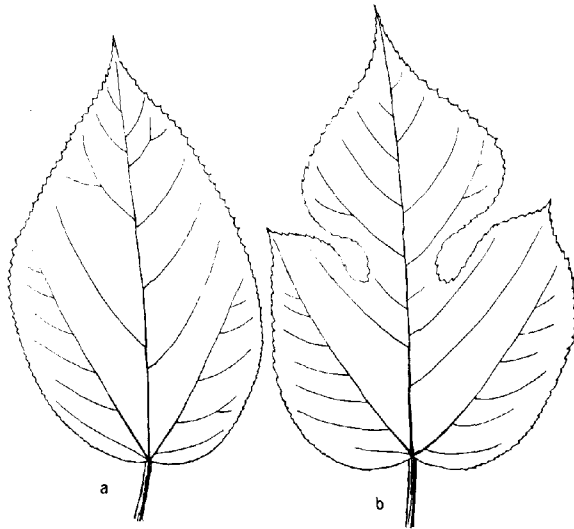


FIG. 34. *Broussonetia papyrifera*. a: leaf from an old tree; b: leaf from a young seedling, one meter tall. Original.

It is of importance, furthermore, which eye of a rose stock is employed in grafting practice, for the gardener knows from experience that buds of very long branches which do not flower produce plants which grow rapidly, to be sure, but which produce few or no blossoms, whereas buds from short flower-bearing twigs yield plants with short flower-bearing axes. To those interested, numerous examples of this and similar phenomena are available in another paper of mine.³⁶¹

If one considers the cases which I have specified and the experience of gardeners in the field of asexual propagation, it becomes clear that the preservation of characteristics in the shoot by means of asexual propagation is a matter of wide-spread occurrence. In some cases such retention of characters is quite apparent, in others

less so, and at times it is not at all recognizable. I have already written³⁰² respecting this that "foliage shoots in many plants and according to their locations on the plants are not always identical, but are more or less individual, and permanently retain their characteristics, their nature, when raised as cuttings." For this phenomenon I propose the term 'topophysis.'



FIG. 35. *Arancaria excelsa*. Original.

"A cutting from the flowering region is more apt to produce blossoms, a terminal slip yields a plant differing permanently from one produced by a lateral axis of higher order, and a root shoot produces plants which have a greater tendency toward root sprouts than do seedlings, and for these reasons the gardener should always give consideration when making cuttings or grafts to the region of the mother plant from which the scion is secured."

It is apparent from our considerations of topophysis* that thyl

*My reference to the "location nature" (Ortsnatur) or "topophysi" brings to mind the investigations of Sperlich³⁰³ on "Phyletische Potenz" which in my opinion are not by any means sufficiently appreciated. The author has shown that the seeds of *Alectorolophus hirsutus* give rise to progeny which are not equally strong and endowed with life. The degeneration of weakened individuals can be manifested by death of the seedlings soon after germination, by abnormal germination, chlorosis, death of the plant before flowering, failure of the flower buds to open, poor development of macrospores or microspores or of both, slow growth, nanism, etc. Furthermore, the seeds of weak individuals are short-lived, for, ac-

growing points of one and the same plant, according to their positions on the plant, are different, and that, furthermore, these points must differ according as they belong to younger or older plants of the same species. Otherwise, it would not be understandable that they produce different plants. These facts lead to the conclusion that the growing point of an individual plant does not remain perpetually unchanged but undergoes changes during the course of time. The growing points grow old, and with advancing age they acquire characteristics which bestow upon shoots developing from them, features that are absent from younger growth or at least not so fully developed.



FIG. 36. *Araucaria excelsa*. Lateral shoot of first order cultivated as a cutting, preserves its lateral habit. From Vöchting.

The foregoing considerations lead to a question which was often asked in the past century as well as during more recent times. Does continued asexual propagation by means of cuttings and graftings bring about weaknesses of old age?

This question has been answered in very contradictory replies, negatively by most theorists, affirmatively by the majority of practicing to the extent of their weakness, they can not withstand prolonged desiccation.

The seeds of an individual have different degrees of "Phyletische Potenz," i.e., unlike capacities to assure the further existence of the species.

"The expression of weakness is dependent upon the order of rank of the capsule bearing the seed and upon the fruiting ability of the individual. The later an individual has arisen, the weaker are its descendants and the sooner must its lineage perish."

Seeds which are developed on side branches, later than those on the main axis, therefore do not give rise to long-lived plants. And on the main shoot itself, the seeds of the lowermost flowers yield a better progeny than do the later blossoms of the upper branches.

It is apparent from these remarks that the phyletic power of the seed of one and the same individual is dependent upon the location of its source upon the plant just as the nature of the shoot varies according to its location on the plant (topophysis).

tical men. The views which were entertained up to about 1854 are summarized in the excellent work of Jessen³⁶⁴ which shows that the opinions were divided. The leading question was: Is longevity unlimited in those plants which are raised from seed and multiplied by asexual propagation (shoots, cuttings or layers of any kind), that is to say, of the individual in the widest sense of the term as conceived by Gallezio,³⁶⁵ terminated only by accident or by unfavorable external conditions before the disappearance of the species itself, or is it definitely limited in duration and subordinate to the species?

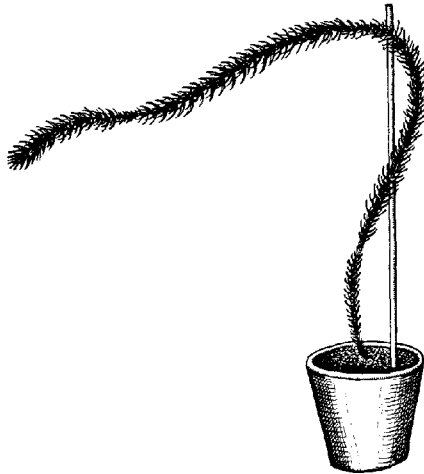


FIG. 37. *Araucaria excelsa*. Lateral shoot of second order cultivated as a cutting, also preserves its lateral nature. From Vöchting.

A plant developing from an embryo, from seed in the case of flowering plants, may be regarded as rejuvenated and refreshed and capable of further perpetuation by production of new seeds. It is a different situation, however, according to Jessen, with respect to plants originating in an asexual manner by buds, cuttings or suckers. In them there is not any rejuvenation and their propagation involves only an extension of the life of the individual, and since this is limited in its duration the progeny of such an individual

must also possess limited tenure of life. In accordance with this view, all plants which originate by asexual increase, *e.g.*, by cuttings, from a plant that has arisen from seeds, are to be regarded as belonging to one individual and are to be designated altogether as a clone.* And just as the individual is subject to the infirmities of old age, so, according to Jessen, is the clone also.

The Englishman, Knight, famed as plant physiologist, gardener and animal breeder, advanced the idea in the first third of the last century that the tree is subject to a natural weakness of old age and that it dies because of internal causes. He, too, was convinced that the scion employed in grafting retains the characters of the mother plant, *e.g.*, its age and associated features. If the condition with respect to age is transmitted through the scion it will be possessed also by the plant arising from such a scion as well as by any other individuals which may in turn be secured by scions from this first plant. Every degree of aging, according to Knight, is transmitted through the scion to the crown which develops upon it, and the scions of a tree unable as yet to produce flowers will not be made to blossom by transference to a stem capable of bearing flowers and fruit; and likewise, the youth of a stock will not prevent flowering of a scion sufficiently mature to do so when transplanted upon it.³⁶⁶

Knight has also made it clear that the life of a variation is prolonged through grafting beyond that of the seedling. Finally, however, vigorous growth declines and there comes a time beyond which the aging process can not continue. According to Knight, old fruit trees, for example, apple trees, easily become cancerous, and if scions are taken from such trees, the disposition toward cancer is readily transmitted through such scions. This opinion is shared also by van Mons.

Jessen concurs with Knight's ideas and after giving detailed attention to the fact that different ailments of our cultivated plants are associated with the infirmities of old age, and after having attempted to weaken the objections of Dochnahl and Overdiek, he declares: "I have no intention of claiming that the cause of the above-mentioned phenomena is either excessive age or prolonged existence of the descendants of a seed plant through layers or removed shoots."³⁶⁷

* The original German word is "Sorte" which ordinarily means a "kind," "variety" or "sort," and it is not clear whether it was intended to carry the meaning of the word "clone" which appears more appropriate in this connection.—E. H. F.

About thirty years ago Moebius³⁶⁸ took a decided position with respect to the ideas of Knight and Jessen. In the chapter dealing with the consequences of continued vegetative propagation he summarizes his ideas in an excellent manner concerning a degeneration occasioned by long continued asexual multiplication. He refers at first to a botanical authority, Schleiden, who said: "In my opinion, healthy human intellect will always find it amusing when it is expected that one should regard the 2000 poplars of a Prussian chaussée, miles in length, as one continuous individual."³⁶⁹ Reference is thus made to the pyramidal poplars of broom-like growth so frequently used along streets, trees which probably represent a variety of the black poplar, *Populus nigra*. These poplars regularly lose their crown tips on different sites and gradually die, and in this manner they perished in England from 1820 to 1840. In America, too, they began to die about 1840, and in northern and central Germany they have frequently become sickly since 1880. This decline and dying-off has been attributed to various causes, among others, climate, cold and parasitic fungi.³⁷⁰ The race of trees known as *Populus italica* Moench (*P. fastigata* Desf.) probably hails from central Asia, whence it came to Italy and from there to other lands. Since the poplars in Germany are almost exclusively staminate trees, they have been propagated only by asexual means, and for this reason the opinion has been entertained by many that this continued practice has led to the weaknesses of old age and to death. As opposed to this, Moebius says he can not believe that a tree should succumb to such weaknesses after less than one hundred years of cultivation.

Concerning this idea I might make the following remarks. In all probability, these trees were introduced about a century ago, not by way of seeds but as cuttings, and if we assume that the cuttings were secured from an old tree, 50 to 100 years of age, we then have every reason to assume, in view of what has already been said, that this age was imparted also to the cuttings. We must admit, therefore, that the clone already was 150 to 200 years old, and if the tree from which the cuttings were originally taken was also derived from an old individual in a similar manner, we must then attribute a still greater age to our present strain, and it is no longer easy to discard the idea of old age decadence. That this decline does not take place simultaneously in all trees, should not

be perplexing, for climatic influences certainly play a rôle in the matter. If, on the other hand, the closely related black poplars have been propagated by means of cuttings since the earliest times of plant cultivation and still remain healthy, it must first be determined whether or not sexual reproduction was interjected at sundry times into the history of this species. Both sexes of *Populus nigra* are known and it is more than likely, therefore, that many trees owe their existence to sexual propagation, involving a refreshing process.

It is well known that the weeping willow, *Salix babylonica*, was brought from the Orient to Europe at the beginning of the last century as a scion of a pistillate tree, and that from this single specimen all other weeping willows now in Europe have been derived. Of this tree, too, it was observed in the early sixties of the last century that its representatives in Germany for the most part had perished. It can be observed today even, as I have often convinced myself, that weeping willows do not attain great age but soon begin to decline. Is it not significant that this condition should have developed not only in the poplar but also in the willow, another tree which has been propagated only asexually? Though we can not prove that there is a weakness accompanying old age, there is, however, much in favor of the idea.

Möebius is opposed also to the view that old age weakness with a definite disposition toward sickness is brought about in vine stock by continued propagation by means of cuttings. He is of the opinion that in this plant which has been cultivated for 5000 to 6000 years, only cuttings have "probably always" been used,³⁷¹ and that there should be indications of old age weakness which there are not. This conclusion is founded upon a false assumption, because in the case of the vine new seedling crosses have been made and a renewed vigor thereby achieved. If we consider the observations of Benedict, already mentioned respecting the progressive narrowing of foliar venation which accompanies advancing age, and give heed also to the matter of topophysis, it becomes clear that in the vine, too, certain characteristics of the aging plant are transmitted to the cutting, and it appears very probable that also in these plants, continued asexual propagation would lead to old age weaknesses and to a lessened resistance toward various diseases. Even though it can be shown that plants derived from seed suffer equally

as much from the fungi causing various diseases of the vine stock as do the cuttings, it obviously does not follow that plants derived from cuttings do not possess a constitution different from that of the seedling.

Moebius also regards Jessen's idea as unfounded according to which the potato suffers old-age weakness as a result of constant asexual propagation and thereby becomes more subject to the fungus disease caused by *Peronospora infestans*. Moebius says in this connection: "All in all, we certainly do not have sufficient grounds for the assumption that multiplication of potatoes by means of tubers leads to a disease of the plant and disposes it toward fungal infection. Rather is it irrefutably shown by what we know about the development of the fungus that it alone causes the diseased condition in the healthy plant."³⁷² I, too, like Moebius, am of the opinion that the cause of the potato disease is the above-mentioned fungus, but it does not follow from this that the potato can not grow old in Jessen's sense through long continued asexual propagation. We must not overlook the fact that from time to time vegetative increase has been interrupted, and that vigor has been restored through seedlings. We can not, therefore, speak of propagation as having been secured exclusively by means of tubers.

Drescher³⁷³ has furnished an historical review of cross-breeding, treating old varieties and flowering relationships of the potato from about 1785 up to the present. These studies show that in order to secure new forms cross-breeding has been resorted to and that great importance has been attached to raising potatoes also from seed. By this means an attempt has been made to put new life into the varieties and to make them more resistant toward disease. "The basis of the greatly increased and constant need for the culture of the varieties of potatoes lies in the degeneration of old forms and in the increased intensity of potato cultivation. Vegetative selection and especially seedling culture have furnished the most valuable varieties with respect to revenue, starch content, and resistance toward diseases and other unfavorable environmental factors. Seedling culture is breeding in a true sense."

Though the potato is usually propagated asexually, seedling culture, too, is thus employed from time to time in the case of old retained varieties as well as in hybrids. The tubers of the seedlings come into the trade and are widely distributed, and good returns,

disease resistance and other qualities have been attributed to the progeny of such tubers. If the potato, therefore, is recorded in the literature as an example of a cultivated plant the propagation of which is exclusively asexual, such claims are not entirely correct.

Many fruit trees are customarily grafted through scions of particular strains and since the scion transferred from an aging tree to a wildling retains the characteristics of the mother plant, sometimes also its age, this practice may lead to the weaknesses of old age, for from such a grafted tree other scions will be taken again and again through many generations. Such a result has already been assumed to occur by Knight and van Mons, but the idea is opposed by Moebius. Several years ago²⁷⁴ I remarked that the last word in this controversy did not appear to have been uttered as yet, and I said that "the scion taken from an old tree displays weak growth and soon produces flowers and fruit; the scion from a young seedling, on the other hand, grows rapidly and produces flowers and fruit only after a longer period, exactly as is to be expected according to the doctrine of shoot individuality or topophysis. This certainly means that the tissue of the growing point derived from an old tree possesses characteristics different from those of a growing point secured from a young tree. In other words, the tissues of the growing point could suffer permanent changes which go hand in hand with the age of the individual."

It is apparent also from their unequal ability to develop roots that the shoots of an old tree possess characters different from those of a young tree. If we make cuttings from an old ivy plant capable of flowering and also from another not yet able to produce blossoms, and stick them in moist sand, we see that the twig of the young plant produces roots very readily under favorable temperature conditions after only one week but that the old plant requires one to three months. I have found this unequal rooting capacity especially striking in seedlings of *Ficus stipulata*. This plant, often cultivated in our greenhouses, possesses comparatively small round leaves during youth. Later, if the plant is in a condition to produce flowers, the form and size of the leaf changes to such a degree that the entire habit is altered and any one unacquainted with the situation would never think that the twigs of the old and the young plant belong to the same species (Fig. 33). On June 12, 1928, cuttings were made from the small-leaved youthful form as well as

from the large-leaved older form and were immersed in water in order to induce root formation. On June 25 the younger form had

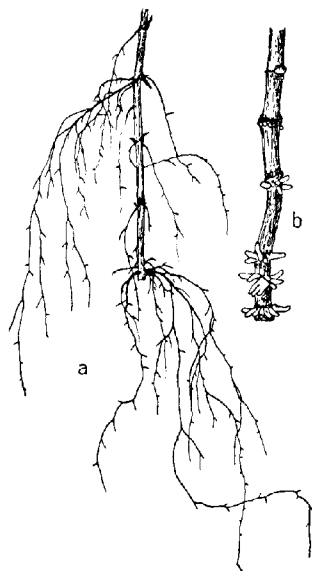


FIG. 38. *Ficus pumila* (= *F. stipulata*). Lower part of a cutting. *a*: from a young plant, producing in water long, delicate, much-branched roots; *b*: from an old plant, producing in water only short cortical outgrowths, but no roots. All after 1½ months cultivation. Original.

roots two centimeters long but the older had none. On July 5 the slender roots of the former were abundant, much branched and ten centimeters long, while the older cutting still showed no roots. Instead, there were snow-white pustules of an aerenchyma-like character around the buds which represented, not root primordia, but parenchymatous outgrowths of the cortex. These later became .2 to 1 cm. long, had a rough surface, and their cells easily lost their coherence (Fig. 38). It was only above water that a few small roots formed in the moist air.

It is well known to the gardener and I have learned by personal experience, that scions for grafting purposes should not be taken from very old trees, because union between the scion and stock is then more difficult than with cuttings from, relatively younger sources. In other words, as soon as a tree

reaches a certain age it is with greater difficulty that its twigs form roots and scar tissue in grafting. It appears doubtful to Doflein,³⁷⁵ however, that old age phenomena occur in old trees and he questions the idea that weak growth exhibited by a scion secured from an old tree is to be regarded as an indication of old age. He believes that nutritional factors which have no direct relation with

age are concerned in such cases. Had Doflein known that a cutting of an old tree manifests all the peculiarities of its old mother—weak growth, immediate flowering capacity, leaf form—as in *Hedera*, *Broussonetia*, *Ginkgo* and *Ficus stipulata*—and additional features of its own, though it develops its own vigorous root system, he would have had no doubts about old age phenomena in plants. One can hardly claim, in attempting to account for this otherwise, that a well-rooted seedling of an old tree is hindered in its nutrition.

Doflein does not regard death from old age among plants as having been definitely established. Emanating from a zoologist this idea is excusable, for to him the facts of the matter are naturally not so well known as they are to the plant physiologist. When this author speaks of the yellowing of leaves and says, "The falling leaf, the foliar corpse, has an entirely different constitution than the living leaf," it is apparent that he regards the yellowed leaf as dead. This is not the case, however, for the leaf becoming detached from the tree is usually alive, as I have already emphasized.³⁷⁶ That the yellowing of leaves in autumn is to be regarded as a matter of old age can no longer be doubted in view of the observations which I have brought forth.

Furthermore, we should probably distinguish between natural asexual multiplication, as takes place normally in the potato, horseradish, banana, *Ranunculus Ficaria*, and others, and artificial asexual propagation, as is accomplished in an abnormal manner by means of cuttings and grafted scions. In the former we are dealing with multiplication rooted in the very nature of the plant, but the latter class involves an artificial situation. There is always the possibility that in those plants which have predominantly or exclusively asexual propagation as a natural and normal means of propagation, the growing point may always be maintained in a youthful condition.

Should I now attempt to summarize all observations in this field, I arrive at the following:

1. The tree is not, as prevailing views would claim, endowed with perpetual life. It, too, is destined to die, though all adversities of its surroundings be completely excluded, for there are facts which indicate that its growing points do not remain unchanged during the course of its life, but also grow old.

2. Continued asexual propagation through cuttings and scions can lead to weaknesses of age because the peculiarities of the mother plant, particularly those associated with old age, are transmitted to the progeny through the cuttings or scions.

Whether old age weakness finally sets in also in those plants which in Nature increase by asexual methods, I can not venture to say.

BIBLIOGRAPHY

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INDICES

BIBLIOGRAPHY

I

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II

Some citations from the more recent literature concerning longevity and related topics discussed in Dr. Molisch's work.

In addition, further study of these subjects must in the future take into consideration certain other topics upon which a voluminous literature has accumulated during recent years, but which at the time of Dr. Molisch's study were either overlooked or had not been developed to such a degree as to merit attention. They include iarovization, auxin, polyploidy, and sex reversal, the study of which phenomena has revealed much that undoubtedly will influence future understanding and interpretation of longevity and associated phenomena. A great portion of the experimental work underlying these revelations has involved artificially controlled and unnatural conditions, and has not been especially concerned with the longevity of plants as they exist in their natural state. For this reason, primarily, an attempt was not made to incorporate these findings in a revised rendition of this book which as a pioneer work in the field was concerned more with plants under natural conditions.

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